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REVISION AND PHYLOGENY OF ANOMODON AND HERPETINEURON (ANOMODONTACEAE, MUSCI)

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INTRODUCTION

The genus *Anomodon* was segregated from *Neckera* Hedw. by Hooker and Taylor (1818). The two species in Hooker and Taylor's new genus, formerly included in *Neckera,* are *A. viticulosus* (Hedw.) Hook. & Taylor and *A. curtipendulus* (Hedw.) Hook. & Taylor, the latter transferred a year later to *Antitrichia* by Bridel (1819: 136).

Bruch, Schimper, and Gümbel (1851–55) assigned *Anomodon*, together with *Leskea*, to the family Leskeaceae, as a segregate family from the Hypnaceae, which still included *Pseudoleskea* BSG, *Thuidium* BSG, and *Heterocladium* BSG. Brotherus (1909) recognized five subfamilies within the Leskeaceae: Thelieae, Heterocladieae, Leskeae, Thuidieae, and Anomodontae. Schimper (1860) had previously recognized the Thuidiaceae at the category of family (as "Thuidiae"), although he included *Anomodon* in the Leskeaceae ("Leskeae"), along with *Myrinia* Schimp., *Myurella* BSG, and *Leskea* Hedw. In the second edition of *Pflanzenfamilien*, Brotherus (1925) recognized the Thuidieae, Leskeae, and Thelieae, all with family rank and, based on gametophytic characters, placed *Anomodon* in the Thuidiaceae. Many modern workers (Gangulee 1978; Iwatsuki 1963; Noguchi 1972, 1974; Nyholm 1960; Smith 1978; Watanabe 1972, among others) have followed Brotherus's treatment by recognizing the three families, sometimes together with the Fabroniaceae, and also acknowledging the order Thuidiales. These authors include *Anomodon* and closely related genera [*Haplohymenium* Dozy & Molk., *Herpetineuron* (Müll. Hal.) Cardot, and sometimes others] within the Thuidiaceae, often in the subfamily Anomodontoideae (or the tribe Anomodontae). In their list of European mosses, Corley et al. (1981), for example, segregate Thuidiaceae and Leskeaceae, and include *Anomodon* and *Haplohymenium* in the former.

Among the authors who have included *Anomodon* and *Haplohymenium* in the Leskeaceae (although the Thuidiaceae are segregated) are Mönkemeyer (1927), who recognizes also the Theliaceae (close to the Fabroniaceae), Crum and Anderson (1981), and also Ireland (1982), although he merged the Theliaceae with the Leskeaceae. The decision to recognize Leskeaceae is most likely based on the poorly branched leskeaceous mosses, devoid of paraphyllia, with erect and symmetric capsules and an imperfect peristome, whereas the Thuidiaceae have much-branched stems covered with abundant paraphyllia and pluripapillose, obscure leaf cells. Neither family (three, if the Theliaceae are considered) seem to be very well defined, but the Thuidiaceae have been segregated from the Leskeaceae on the basis of their inclined, slightly asymmetric capsule with a perfect, hypnaceous peristome (Crum 1976).

Anomodon and its closely related genera do not fit clearly into either family. The gametophytic characters lead to the placement of these genera among the Thuidiaceae, whereas the sporophytic ones suggest a closer relationship to the Leskeaceae. The capsules are erect and the peristome is not perfect, although in some species the exostome is horizontally striate at the base. The segments, on the other hand, are not keeled, the cilia are rudimentary or absent, and the basal membrane is no more than 3 cells tall or, in most species, absent. These sporophytic characters and the lack of paraphyllia suggested to Crum and Anderson (1981) and Ireland (1982) a relationship with the Leskeaceae sensu stricto. According to Brotherus (1925), the profusely branched stems, the pluripapillose and obscure leaf cells, and the presence of horizontal striae on the exostome indicate a closer relationship with the Thuidiaceae. This opinion has been followed by Crosby and Magill (1978, 1981), Smith (1978), Corley et al. (1981), Düll (1985), and many others. Other authors, like Limpricht (1895), Dixon (1924), Grout (1903, 1932–1934), Bartram (1947, 1949), and Crum (1976), have adopted a more conservative classification, considering the Leskeaceae sensu lato, with the Thuidiaceae subordinated within.

Crosby (1980), Vitt (1984), Buck and Vitt (1986) and, Buck and Crum (1990) propose different arrangements for the genera within the Thuidiaceae and the related families Leskeaceae and Theliaceae (including *Anomodon* and closely related genera). Watanabe (1972) recognized the subfamily Anomodontoideae, in which he included *Miyabea* Broth., *Haplohymenium*, *Anomodon*, and *Herpetineuron*. Buck and Vitt (1986) excluded the Anomodontaceae (comprising *Anomodon*, *Herpetineuron*, *Thelia* Sull., *Myurella* BSG, and *Lindbergia* Kindb.) from either family and placed them closer to the Leptodontaceae and Cryphaeaceae (superfamily Cryphaeacanae). The three families share the character ("homoplasic") of having a costa, which distinguishes them from the Leucodontaceae and Hedwigiaceae. However, the straightforward rearrangement of the Thuidiaceae and Leskeaceae by Buck and Crum (1990) definitively removes the Anomodontaceae from the Leskeaceae alliance, and places it close to the Cryphaeaceae, in the Leucodontales, based on peristome morphology, presence of a creeping primary stem, and leaf areolation. The most representative characters of the Anomodontaceae are absence of paraphyllia and presence of papillae in the lamina cells (probably secondarily lost in *Herpetineuron* and other taxa), as well as epiphytic and epilithic habitats. In addition, the peristome of the Leskeaceae, although somewhat reduced, is essentially hypnaceous and differs from that of the Anomodontaceae. Akiyama (1988), and more recently Anderson et al. (1990), present in their North American list a rather similar position for the family Anomodontaceae. They include it in the order Leucodontales, but they place Theliaceae, Leskeaceae, and Thuidiaceae quite close to each other within the Hypnales. The novelty within Anomodontaceae is the addition of *Pterogonium* as a fourth genus, with *Haplohymenium*, *Anomodon* and *Herpetineuron*. Enroth (1992) included two other monotypic genera in the Anomodontaceae, transferred from the Neckeraceae: *Chileobryon callicostelloides* (Thér.) Enroth and *Bissetia lingulata* (Mitt.) Broth., the latter species lacking papillae and with a very short costa.

The most complete taxonomic work for the genus *Anomodon* is by Iwatsuki (1963), for the East Asiatic taxa. Iwatsuki reduced the 14 taxa then recognized for the region (Sakurai 1954) to 9 species and 2 subspecies. He included *Anomodon* in the family Thuidiaceae.

The purpose of this paper is to provide a comprehensive taxonomic treatment for all the species in *Anomodon* and a phylogenetic analysis for the genus as it is known today, but including also the other taxa in the family Anomodontaceae, at least those represented by a sufficient number of collections. The revision of the genus *Haplohymenium* by Noguchi (1957) has been the starting point for the analysis regarding the species in this group.

PHYLOGENETIC ANALYSIS

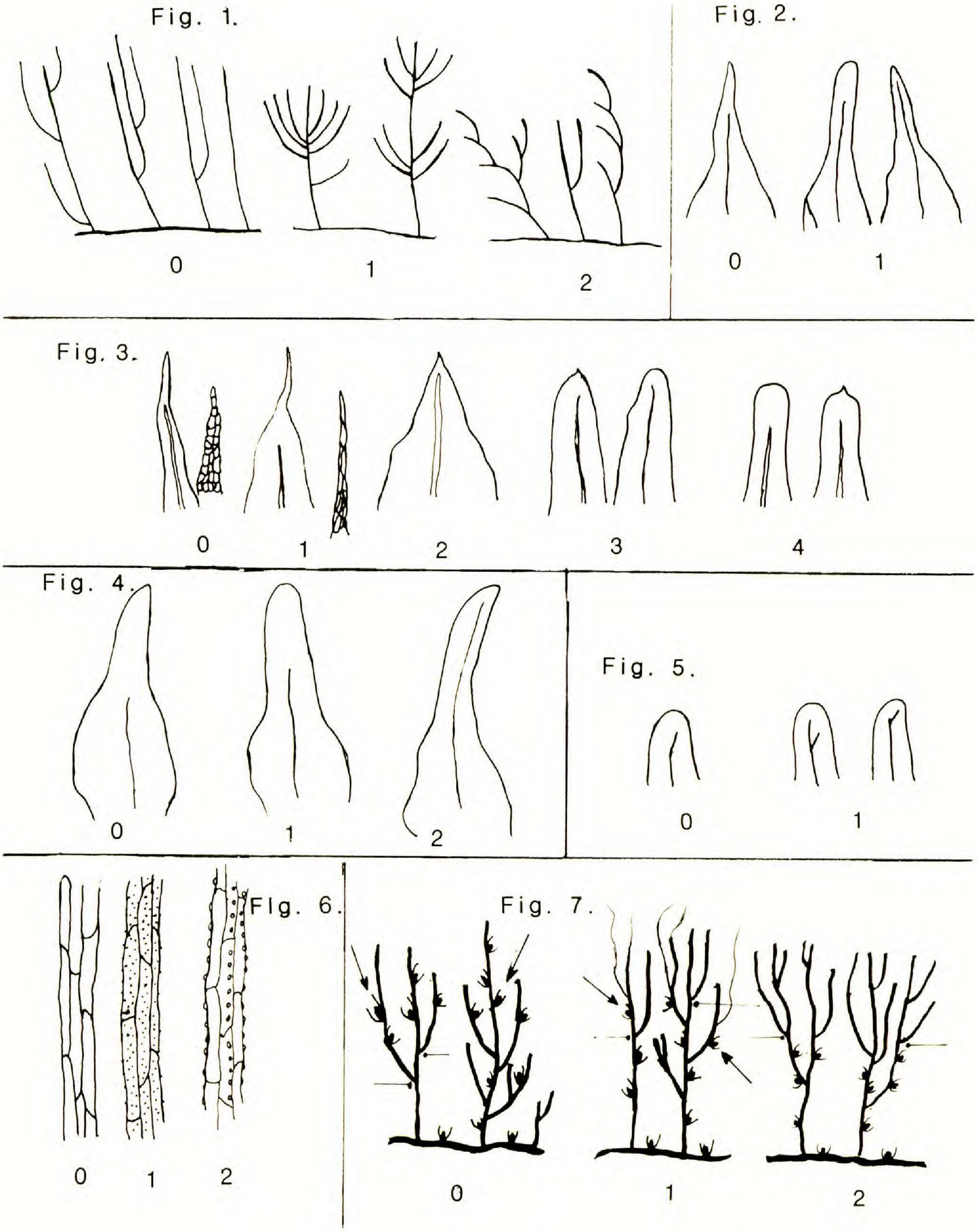
MATERIALS AND METHODS

In preliminary analyses in which *Haplohymenium* and *Herpetineuron* were used as outgroups, *Haplohymenium* consistently turned out to nest within the ingroup. Consequently, three outgroup taxa were used: *Herpetineuron toccoae* and *H. acutifolius*, in addition to *Pterogonium gracile*, following Akiyama (1988) and Anderson et al. (1990), who include *Pterogonium* in Anomodontaceae.

The taxa included in the analysis are all eleven species of *Anomodon*: [*A. abbreviatus* Mitt., *A. attenuatus* (Hedw.) Hüb., *A. dentatus* Gao, *A. giraldii* Müll. Hal., *A. longifolius* (Brid.) Hartm., *A. minor* (Hedw.) Lindb., *A. rostratus* (Hedw.) Schimp., *A. rugelii* (Müll. Hal.) Keissl., *A. solovjovii* Lazarenko, *A. thraustus* Müll. Hal., *A. viticulosus* (Hedw.) Hook. & Taylor] and five species of *Haplohymenium*, considered as part of the ingroup [*H. longinerve* (Broth.) Broth., *H. pseudotriste* (Müll. Hal.) Broth., *H. sieboldii* (Dozy & Molk.) Dozy & Molk., *H. triste* (Ces.) Kindb., *H. flagelliforme* Savicz-L.]. The outgroup comprises *Herpetineuron toccoae* (Sull.) Cardot, *H. acutifolium* (Mitt.) Granzow-de la Cerda, *Pterogonium gracile* (Hedw.) Sw.

Characters were coded based on an examination of herbarium specimens; additional information was obtained from descriptions of Brotherus (1925), Crum and Anderson (1981), Grout (1932–1934), Iwatsuki (1963), Noguchi (1957), Sullivant (1864), and Watanabe (1972). Some characters were considered unordered, and character 11 (shape of leaf apex) was assigned a stepmatrix (see Appendix 1). Schematic drawings for some characters are provided in Figs. 1–7. Trials with different character weighting criteria were run: (1) a character scaling was applied in order to assign the same weight to all characters, regardless of number of states (base weight = 4, as characters present had 2, 3, or 5 states); (2) equal weight (= 1; weight becomes dependent on the number of character states). The 31 characters used are discussed below (Appendix 1); the data matrix is shown in Appendix 2. Autapomorphic characters were not included in the analyses.

The cladistic analyses were conducted using PAUP (Version 3.0r, for the Macintosh computer, Swofford, 1990) on the 19 taxa and 31 characters. Heuristic searches were carried out using random stepwise addition option and the TBR (tree bisection reconnection), branch swapping option, keeping all most parsimonious (shortest) trees found. Strict consensus trees were computed for all trees obtained at the end of each analysis. As a measure of support to evaluate the relative robustness of the clades, "Bremer support" (Bremer 1988, 1994; Källersjö et al. 1992) or the "decay index" (Mishler et al. 1991; Donoghue et al. 1992) was determined. Heuristic searches retaining trees progressively longer by one step were run, until their strict consensus rendered a tree that was totally unresolved.



FIGS. 1–7. Schematic representation of states in some characters, as coded for the cladistic analysis. Fig. 1. Character 1, branching pattern. Fig. 2. Character 9, shape of the distal region of the lamina of branch leaves, above the shoulders. Fig. 3. Character 11, shape of the branch leaf apex. Fig. 4. Character 13, length of the costa. Fig. 5. Character 14, bifurcation of the costa near the apex. Fig. 6. Character 16, papillae of dorsal surface of the costa. Fig. 7. Character 21, position of gametangial buds relative to most recent (distal) branching points.

RESULTS

Three most parsimonious trees, 325 steps long, with consistency index of 0.44, were obtained when scaling was applied (analysis 1). Their consensus tree is given in Fig. 8a. When equal unit weight was applied, without scaling (analysis 2), four trees were generated, their length 121 steps and consistency index 0.45. The strict consensus tree for analysis 2 is given in Fig. 8b, and Fig. 9 shows one of its four most parsimonious trees. Within the ingroup, two major clades can be distinguished in these trees. One consists of the taxa *A. attenuatus*, *A. giraldii*, and *A. longifolius*, and in half of the trees *A. rostratus* is also included (these species constitute the subgenus *Pseudoanomodon* Limpr.) The other clade is made up of the remaining species of subgenus *Anomodon*: *A. viticulosus*, *A. rugelii* and *A. minor* (subsection *Anomodon*), in addition to *A. abbreviatus* and *A. solovjovii* (subsection *Abbreviati* Iwats.), *A. dentatus,* the species of the genus *Haplohymenium* (=*A*. section *Haplohymenium*), and *A. thraustus*. *Anomodon rostratus* appears as a sister species in the other half of the trees. This particular species presents an ambiguous position: in two of the trees is part of the basal clade (with *A. attenuatus*, *A. giraldii*,and *A. longifolius*) and in the other two as the sister taxa for the *Anomodon* s. str. clade. The *Haplohymenium* clade always appears as a monophyletic clade nested within *Anomodon* s. str., as in all analyses performed previously (Granzow-de la Cerda 1988b, 1989a). Whether character scaling (analysis 1) or equal weighting of all characters was used (analysis 2), the topologies, as well as consistency indices, remained rather similar. The outgroup (*Herpetineuron* and *Pterogonium*) always remain external.

The values for the Bremer support, or "decay index", for each monophyletic group are given in the strict consensus tree of Fig. 10a. This value indicates how many parsimony steps must be loosened before that branch disappears (becomes unresolved). Figs. 10b and 10c. show trees for which parsimony has been relaxed one and two steps, respectively. At a length of 124 steps (parsimony relaxed by 3 steps) all branches collapsed, therefore no single clade had a support greater than three.

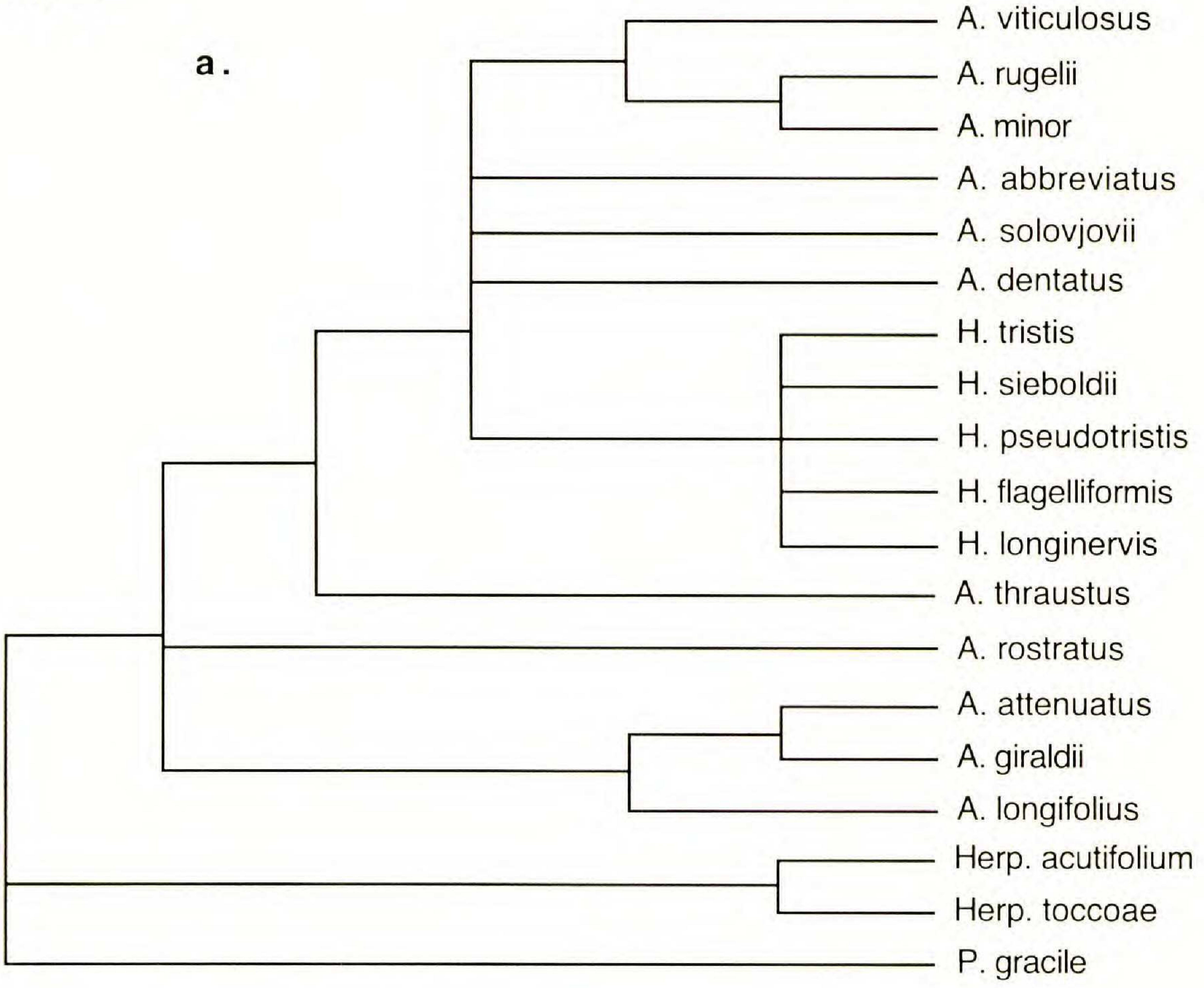
DISCUSSION

Haplohymenium appeared in all cladograms as part of the ingroup, always between two groups of *Anomodon* species. The differences in the cladograms obtained here, as compared to the ones from a previous analyses (in which two species of *Thelia,* instead of *Pterogonium gracile,* were used along with *Herpetineuron* as outgroups; Granzow-de la Cerda 1988b, 1990), are the result of using *Pterogonium* as an outgroup, which seems a more likely close relative to the Anomodontaceae (Akiyama 1988). According to these analyses, *Anomodon* is monophyletic when *Haplohymenium* is included within it.

Although the consistency indices, 0. 44, and 0.45, for analyses 1 and 2 respectively, may be seen as rather poor, they are considerably larger than would be expected given random data for the same number of taxa and characters (Sanderson & Donoghue 1989; Klassen et al. 1991). Moreover, the most parsimonious topologies are quite robust, as they basically remain unmodified under different character weighting procedures; the two main clades are well supported as measured by their decay index or Bremer support (number of steps that parsimony must be relaxed before a group, i.e., a monophyletic clade, disappears; Bremer 1988, 1994; Donoghue et al. 1992; Källersjö et al. 1992), as shown in Fig. 10. The clades corresponding to the whole genus *Anomodon*, and to the subgenus *Anomodon* are the most robust, or best supported, as parsimony needs to be relaxed three steps in order to make those branches collapse).

Taxonomic implications. Iwatsuki (1963), in his monograph of Eastern Asian species of *Anomodon*, places *A. viticulosus*, *A. rugelii*, *A. minor*, *A. thraustus*, *A. solovjovii,* and *A. abbreviatus* within subgenus *Anomodon.* This group of species,

Figure 8.



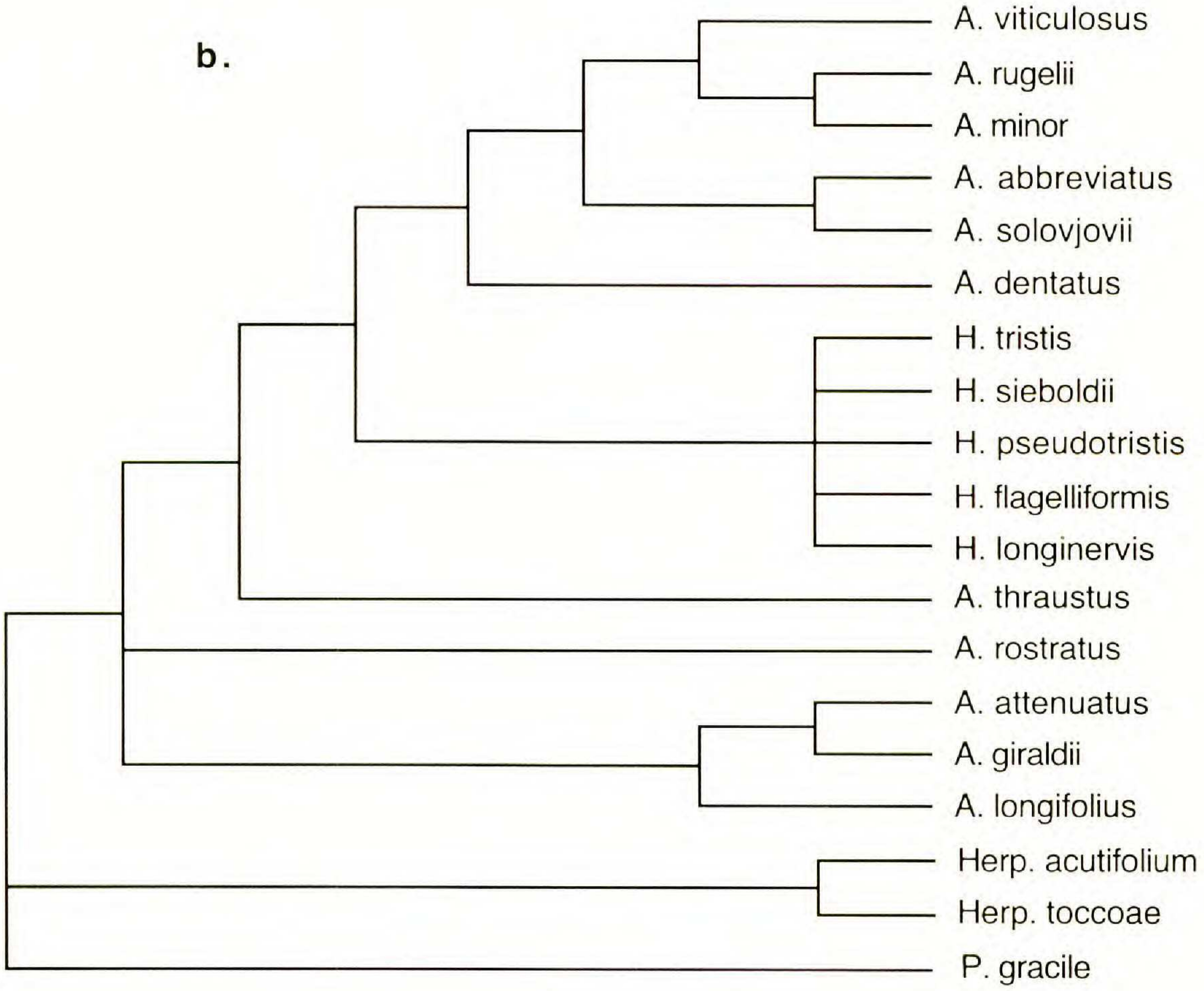


FIG. 8. Strict consensus trees: a, consensus tree for analysis 1 (scaling at 4) of the three most parsimonious trees (325 steps); b, consensus tree for analysis 2 (no scaling) of the four most parsimonious trees (121 steps).

Figure 9.

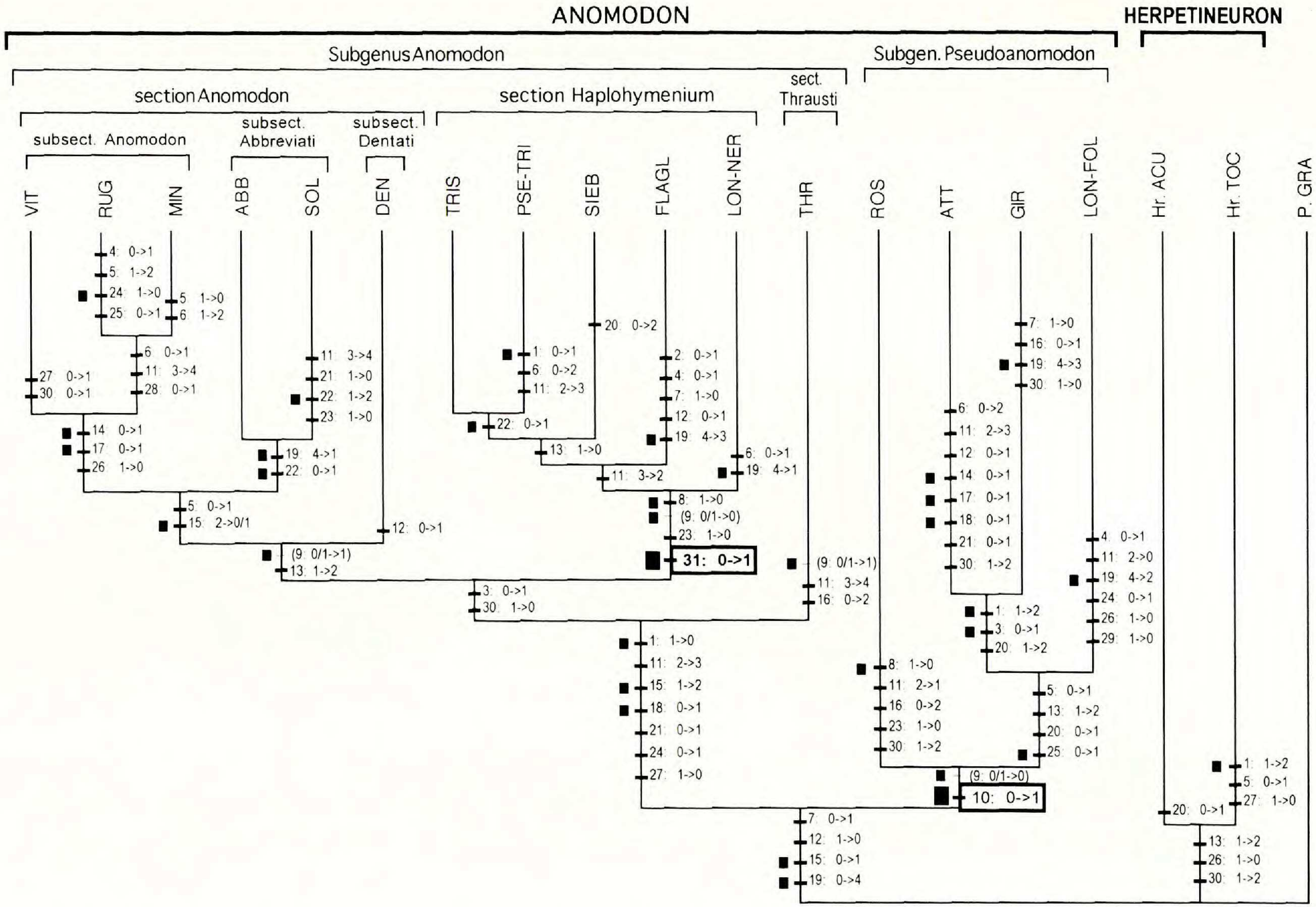


FIG. 9. One of the most parsimonious trees in analysis 2, which assigned equal weights (no scaling). Only unequivocal changes for this particular tree are represented (in addition to character 9). All of them, except for characters 31 and 10 (boxed), are homoplasies. Transformations with a black square show characters with consistency index of 0.5 or higher for this tree. Proposed taxonomic arrangement is also given above the species names.

Figure 10.

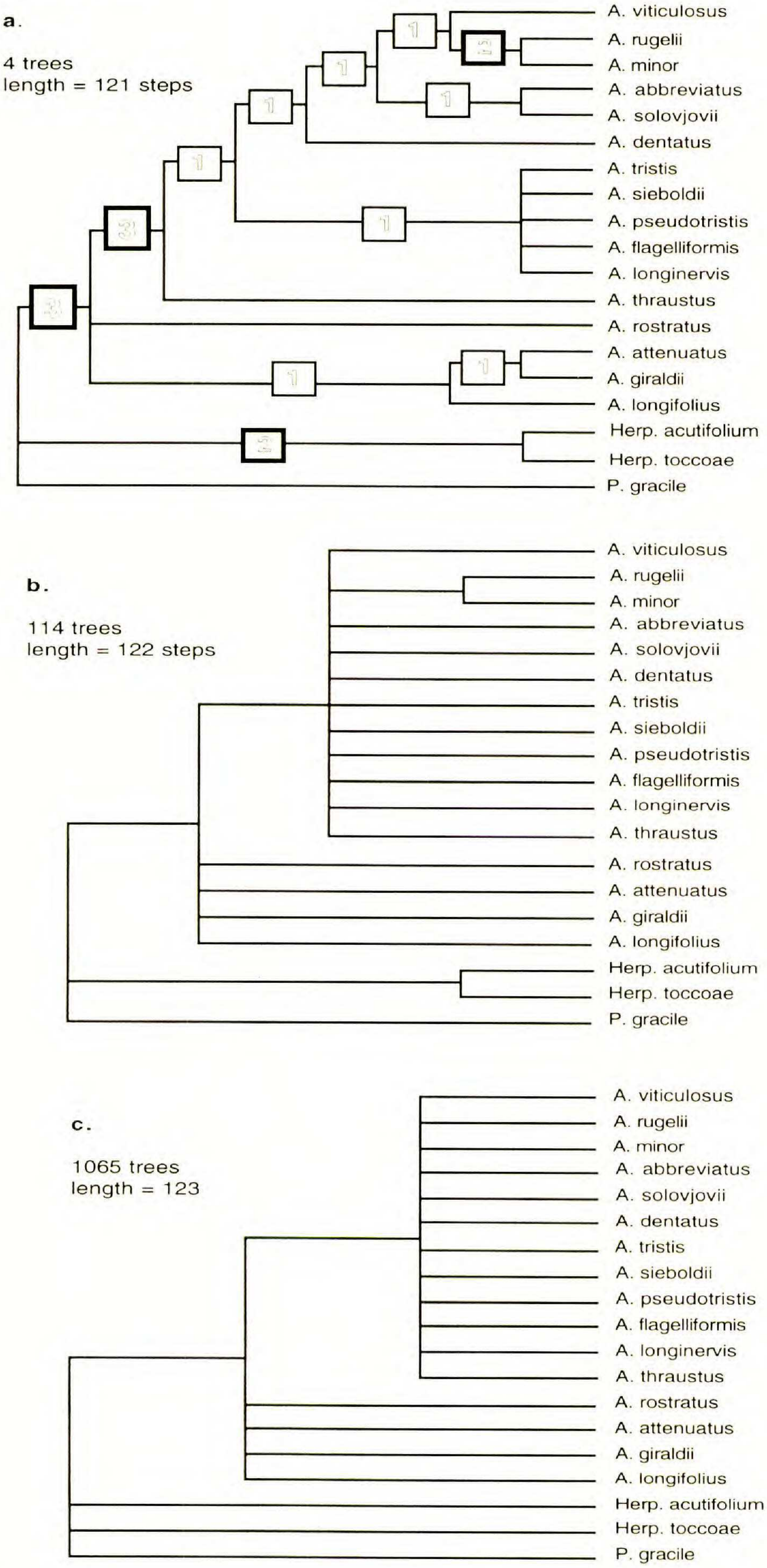


FIG. 10. Bremer support analysis of the four most parsimonious trees resulting of analysis 2 (no scaling). Strict consensus trees become progressively more unresolved as parsimony is relaxed. a, boxed numbers denote how many steps parsimony had to be relaxed to cause that clade to collapse (become unresolved) as an indication of the decay index: clades marked 3 are the most supported (robust), and those marked 1 the least supported; b, tree resulting from parsimony relaxed one step; c, tree resulting from parsimony relaxed two steps. Length and number of trees are given.

if *A. dentatus* (described 14 years after Iwatsuki's treatment) and *Haplohymenium* are included, coincides exactly with what I have come to call the subgenus *Anomodon* clade. According to the analysis 2 (Figs. 8b, 9), subsection *Abbreviati* Iwats., within subgenus *Anomodon*, is composed of those species with a solitary high papilla on each leaf cell, *A. abbreviatus* and *A. solovjovii*. These two taxa appear in the cladograms as the sister group of the terminal clade (*A. viticulosus*, *A. rugelii*, and *A. minor*). *Anomodon thraustus*, now in its own section, consistently appears at the base of the subgenus *Anomodon* clade, which indicates a closer relationship to *Haplohymenium* rather than to *A. minor*, a taxon with which it is often confused. The monotypic section *Auriculati* Iwats. (with *A. rugelii*) is superfluous, given that in all analyses (including preliminary ones) *A. rugelii* appears as a sister species of *A. minor* in a rather robust clade. Subgenus *Pseudoanomodon* Limpr. consists of *A. attenuatus*, type species for the subgenus, *A. longifolius*, and *A. rostratus* (Podpera 1954) in addition to, according to Iwatsuki (1963), *A. giraldii* and *A. acutifolius* (=*Herpetineuron acutifolium*; see Granzow-de la Cerda, 1989a). This subgenus coincides with the other monophyletic clade, when *A. rostratus* is included. Such dual positioning of *A. rostratus* at the base of either clade, however, introduces some ambiguity regarding its relationship with one or the other group.

It can be inferred that according to the traditional treatment of *Anomodon* (i.e., excluding *Haplohymenium*), the genus is paraphyletic. Consequently, only a group of species of *Anomodon* (i.e., subsections *Anomodon*, *Abbreviati*, and *Dentati*, Fig. 9) is monophyletic, with *Haplohymenium* and *A. thraustus* as part of a sister group. Therefore, in agreement with the cladistic orthodoxy, the taxonomic alternative available for the Anomodontaceae is to include the species of *Haplohymenium* within *Anomodon*; the thus enlarged *Anomodon* does form a monophyletic clade.

Herpetineuron acutifolium (Granzow-de la Cerda 1989a) was recently proposed by Enroth (1991) as belonging to *Bryonorrisia* Stark & Buck. The resulting phylogeny, nonetheless, ratifies the close relationship between *Bryonorrisia* and *Herpetineuron*; *H. acutifolium* consistently appeared in all analyses paired together with *H. toccoae*. When Stark and Buck (1986) described *Bryonorrisia* (*B. secunda* Stark & Buck), they placed it in the Anomodontaceae and acknowledged a very close relationship to *Herpetineuron*. In spite of Enroth's emphasis on "the yellowish colour of the exostomes" of *Bryonorrisia*, I do not see relevant differences between these two genera and therefore regard both as one genus. The lack of leaf cell papillae in *Herpetineuron*, as well as in *Pterogonium*, is not sufficient for not considering these genera to be the closest sister group(s) of *Anomodon*, or part of the Anomodontaceae.

Considerations about the characters. There are no real synapomorphies for the *Herpetineuron* clade, and the lack of leaf papillae is a plesiomorphy. Within the ingroup, the hairiness of the calyptra (character 31) is the only true synapomorphic character shared by all species in the *Haplohymenium* clade in all analyses. No other character is consistently synapomorphic, although character 10 (margins flat or revolute) appears as a synapomorphy only in some trees. Unambiguous characters for this particular tree, with their corresponding transformation, are indicated in Fig. 9; those with a consistency index of 0.5 or over are marked with a black square.

Other shared characters for the *Haplohymenium* clade, besides the hirsute calyptra (character 31, Appendix 1 and Fig. 9), are the more reduced habit of the gametophyte (this character not included in these analyses) and the smaller leaves, shorter than 0.7 mm (character 8, although not an actual synapomorphy because it also appears in *A. rostratus*). These characters could explain the predisposition to segregate these taxa into a different genus, *Haplohymenium*, on the basis of what seems a purely phenetic criterion. The state of having the end of the costa obscured by laminal cells for a good part of its upper portion (character 15, state 2), is shared by *A. thraustus*, *A. dentatus*, and, although not so strikingly, by the *Haplohymenium* clade. However, the condition of having a delicate leaf with the apex broken off (excluded from the analyses represented in Figs. 8–10; its inclusion has no effect on the number of trees, their topologies, or consistency) seems to have appeared independently in *A. thraustus*, *H. triste*, and *A. dentatus*.

Geographic distribution. The Asian Far East (Manchuria, Korea, Japan) and the Himalayas are the regions where *Anomodon* is best represented (nine species); only five species occur in Europe and six in the New World.

Subgenus *Pseudoanomodon* clade (Fig. 9). *Anomodon attenuatus* and *A. rostratus* are not found in East Asia but occur in Europe, east to the Caucasus (*A. attenuatus* present also in Kashmir), and in North and Central America. Both are the only species in the genus in the Caribbean islands and Bermuda. The ranges of *A. giraldii* and *A. attenuatus*, on the other hand, apparently do not overlap, although in all topologies generated they appear as sister species. *Anomodon longifolius* has a wide distribution throughout Eurasia, yet it is absent from the American continent.

Subgenus *Anomodon* clade (Fig. 9). Little correlation between phylogenetic position and distribution can be seen in this clade. Two of the terminal species, *A. viticulosus* and *A. rugelii*, are the most cosmopolitan; they both occur in Eurasia as well as in North America, but are more northern than any of the extra-Asiatic species. *Anomodon viticulosus* has been reported from Algeria and the Canary Islands (Dixon 1924), but these reports are most likely erroneous (for the SW Mediterranean distribution, see Granzow-de la Cerda, 1988a). In America, *A. rugelii* does not reach farther south than Georgia and Arkansas. I have seen specimens of *A. viticulosus* from southern Mexico; Gier (1980) also indicates its presence in Mesoamerica but gives no further information. Those localities are probably the southernmost limit of its range.

The other species in the section *Anomodon* are restricted to the Asian Far East: *A. solovjovii* from Manchuria, Henan province in eastern China, and Korea, and *A. abbreviatus* restricted also to Manchuria and Korea, as well as to Japan. *Anomodon dentatus* is endemic to Manchuria. Very different distribution patterns are seen in the taxa from the *Haplohymenium* clade. *Anomodon sieboldii* and *A. longinervis* are known from Eastern Asia, and *A. pseudotristis* occurs in South Africa and Madagascar, East and Southeast Asia, Australia, New Zealand. *Anomodon tristis* is a cosmopolitan species, present in Asia, South Pacific, Europe (although rare), and North and Central America (U.S.A., Mexico, Costa Rica). It has been recorded from the Bolivian Andes under the synonym *Anomodon fragillimus* Herz. (!; Granzow-de la Cerda 1988b, 1989a;). The *Haplohymenium* clade is, therefore, the only one within *Anomodon* with representatives in the Southern Hemisphere (including southern Africa, South America, Australia, and New Zealand).

The basalmost species in the subgenus *Anomodon* clade, *A. thraustus*, shows a disjunct Asian-Mesoamerican distribution, quite similar to that of *A. minor*. *Anomodon thraustus*, however, has a much more restricted range; it is found, in the New World, only in Mexico, whereas *A. minor* is common and occurs from Canada to Guatemala.

Outgroups. Within the *Herpetineuron* clade, *H. toccoae* is quite widely distributed: South and East Asia, from the Himalayas to New Caledonia and the Philippines, south-east Africa, and throughout the American continent, but is absent in Europe (see Kis, 1985, and Norris & Sharp, 1961). *Herpetineuron acutifolium* is more restricted, occurring only in the Himalayas and East Asia (Iwatsuki 1963; Gangulee 1973; Granzow-de la Cerda 1988b, 1989a), but is also present in northern Mexico. It shares with *A. thraustus* a similar disjunct distribution pattern.

Conclusions

All the species of *Anomodon* (s.l.) are grouped in two main clades (Fig. 9) that correspond to the traditional grouping into two subgenera, *Anomodon* and *Pseudoanomodon* Limpr. *Anomodon rostratus* occupies a somewhat ambiguous position, because in some topologies it appears as a sister species for subgenus *Anomodon.*

The genus *Anomodon* constitutes a monophyletic group only when species of *Haplohymenium* are included. *Haplohymenium* Dozy & Molk. (Musci frond. ined. Archip. Indici 4: 127. 1846) therefore needs to be subordinated to *Anomodon*, as supported by the cladistic analysis. All five species of *Haplohymenium* have been studied, and they form a monophyletic clade with well-defined synapomorphies. A change in the taxonomic category to treat these species as a section is appropriate and *Anomodon* section *Haplohymenium* (Dozy & Molk.) Granzow is here proposed (including *A. sieboldii*, the type species for *Haplohymenium*). Three of the species had previously been placed into *Anomodon*: *A. longinervis* Broth., *A. pseudotristis* (Müll. Hal.) Kindb., and *A. tristis* (Ces.) Sull. & Lesq. (as recognized by Noguchi,1957, in his revision of *Haplohymenium*). *Haplohymenium formosanum* is considered here a synonym for *Anomodon tristis* Ces. Two new combinations are proposed for the remaining taxa: *Anomodon sieboldii* (Dozy & Molk.) Granzow and *Anomodon flagelliformis* (Savicz-L.) Granzow.

The remaining sections within subgenus *Anomodon*, besides *Haplohymenium*, are the monotypic section *Thrausti* and section *Anomodon*. The monotypic section *Auriculati* proposed by Iwatsuki (1963), which includes only *A. rugelii*, is superfluous (Fig. 9). On the other hand, if *A. abbreviatus* and *A. solovjovii* (which have been shown consistently to be monophyletic in most analyses) are to be grouped, the appropriate ranking, rather than at the sectional level (sect. *Abbreviati* Iwats.), should be as subsection *Abbreviati*, a sister group to the subsection *Anomodon* clade, also very consistent in all analyses. Accordingly, *A. dentatus*, the basal taxon within section *Anomodon* (a sister species to subsections *Abbreviati* and *Anomodon*, Fig. 9), must be assigned to its own subsection *Dentati*, in compliance with taxonomic orthodoxy.

TAXONOMY

Anomodon Hook. & Taylor, Musc. Brit. 79, pl. 3. 1818.—Type: *Anomodon viticulosus* (Hedw.) Hook. & Taylor.

Delicate to robust pleurocarpous mosses, forming more or less glaucous-green, yellowish, or brownish dense or loose mats, freely branched and irregularly pinnate from a creeping stem. Paraphyllia absent. Stem leaves minute and scalelike, costa thick, usually pellucid, ending below the apex; secondary stem and branch leaves differing in size and shape. Secondary stem and branch leaves similar, ovate to lanceolate at base, more or less abruptly narrowed toward the middle (above or below), distal portion above the shoulders with parallel margins to tapering, sometimes narrowly so (in *A. longifolius*); leaf cells with one to several, mostly well-developed papillae on both surfaces, small, hexagonal, thin-walled and obscure to irregular, somewhat incrassate and pellucid (in *A. giraldii*), at the base oblong, incrassate, smooth, and pellucid. Dioicous. Perichaetial leaves differentiated, narrow and longer than vegetative leaves. Seta long, to 20 mm, flexuous (except for *A. abbreviatus* and *A. solovjovii*, ca. 1–2 mm), reddish. Capsule symmetric, ovoid, cylindrical to oblong-cylindrical, sometimes with stomata; operculum conic to obliquely rostrate; peristome incomplete, exostome white to pale brown, narrowly lanceolate, densely papillose, occasionally cross-striolate and sometimes slightly trabeculate; endostome sometimes very reduced or absent (sect. *Haplohymenium*), usually not keeled, pale with low basal membrane, delicately papillose, with linear segments more or less reduced, cilia absent or nearly so. Calyptra cucullate, smooth or hirsute (sect. *Haplohymenium*). Spores 9–20 (–23) µm in diameter.

All species of *Anomodon* are dioicous. In North America, at least two, *A. rostratus* and *A. attenuatus*, fruit profusely. On the other hand, *A. rugelii* and *A. minor* fruit less abundantly and perhaps less frequently; sporophytes of *A. viticulosus* and *A. tristis* are extremely rare in North America (only one fertile specimen of *A. viticulosus* seen, none of *A. tristis*). In Europe, however, *A. viticulosus* is the most common species and often produces sporophytes.

The species of *Anomodon* grow on tree trunks, including the base, and on logs, soil, or rock (mostly calcareous). In North America, they are an important element of the eastern deciduous forest. It is remarkable how often several of the species grow together yet remain taxonomically distinct. Three of the North American species, *A. attenuatus*, *A. rostratus*, and *A. minor*, and sometimes a fourth, *A. rugelii*, may grow on the same tree, each usually forming its own mat, but overlapping at the margins of mats. The gametophytes of several species may be intertwined in mixed mats. The different species may be found growing intermixed only occasionally. Although a high rate of sporophyte production is observed in some species, no hybrid sporophytes have been recorded.

KEY TO THE SPECIES OF ANOMODON

1. Plants very slender, delicate, stems <0.5 mm thick when dry, leaves <1.2 mm long, differentiated basal cells few, not reaching the margins; calyptra hirsute.
    2. Laminal cells with numerous short, mostly branched papillae, costa short, not extending beyond the proximal 1/3 of the lamina.
        3. Leaves complanate when moist, apex of leaves on non-flagelliform branches obtuse to rounded, papillae inconspicuous. 9. *A. pseudotristis*.
        3. Leaves not complanate when dry, apex of leaves acute to acuminate, occasionally obtuse, papillae conspicuous.
            4. Plants extremely delicate and slender, stems ca. 0.2 mm wide, some becoming flagelliform, <0.1 mm wide at the apex; leaves squarrose, leaf apex tapering into a long awn (plants rare; Manchuria). 10. *A. flagelliformis*.
            4. Plants ± delicate, stems ca. 0.4 mm wide throughout; leaves erect to slightly spreading, leaf apex acute to acuminate, occasionally obtuse.
                5. Leaves invariably broken off for more than 1/2 their length, with an obvious constriction, apex acute to acuminate, occasionally obtuse; costa ending near the leaf constriction; laminal cells with strong, high, branching papillae to mammillose, margin crenulate near the apex owing to protruding papillae. 7. *A. tristis*.

5. Leaves not broken off, with a faint constriction, apex acute but not acuminate; costa reaching well beyond the leaf constriction; laminal cells with delicate, branched but not high papillae, never mammillose, margin smooth. 8. *A. sieboldii.*

2. Laminal cells with 1–2 (–3) rather high mammilla-like, acute, unbranched papillae, costa extending beyond the proximal 2/3 of the lamina. 11. *A. longinervis.*

1. Plants somewhat slender to robust, >0.8 when dry, leaves usually >1.4 mm long (in *A. thraustus* as small as 1.2 mm long), differentiated basal cells almost reaching the margins and extending to ± 1/3 of the lamina; calyptra smooth.

6. Cells of the lamina with a single, long conical papilla, never branched, but sometimes with 0–3 short "spurs" at the base.

7. One single papilla on each cell, low and rounded, without basal "spurs"; the height of the papilla not more than the laminar cell's diameter in cross section; leaves slender, long-acuminate, somewhat subulate, with revolute margin, at least at the transition to the narrower distal portion; pseudoparaphyllia present. 16. *A. longifolius.*

7. Papillae with 0–3 basal spurs, sharply conical, pointing toward the leaf apex; the height of the papillae greater or equal to the diameter of the cell in cross section; leaves obtuse or acute but not acuminate; pseudoparaphyllia absent.

8. Leaves >2.8 mm long, the distal portion (beyond the constriction) tapering, apex acute or obtuse; seta >2.5 mm, capsule exserted. 4. *A. abbreviatus.*

8. Leaves <2.0 mm long, the distal portion (beyond constriction) lingulate, flat and with rounded apex; seta ca. 1 mm long, capsule enclosed within the perichaetial leaves, which are longer than vegetative leaves. 5. *A. solovjovii.*

6. Cells of the lamina with multiple, often more or less branched papillae.

9. Plants glaucous, profusely and irregularly branched, branches julaceous, erect; leaves <0.8 mm long, appressed, the apex extended into a long awn. 13. *A. rostratus.*

9. Plants more or less dark green to rusty brown, with secondary branches loosely spreading to erect, sometimes irregularly pinnate, branches never julaceous; leaves >(1.2–) 1.5 mm long, appressed or not, the apex rounded, obtuse, acute, or apiculate, without an awn.

10. Branch leaves lanceolate, acute at apex, with unbranched papillae; cell walls conspicuously sinuose throughout the lamina; margins revolute. 15. *A. giraldii.*

10. Branch leaves lingulate (or lanceolate in *A. attenuatus*), obtuse or rounded at apex, with branched papillae that obscure the cells; cell walls straight but sometimes sinuose in the basal hyaline cells; margins plane.

11. Plants dark green to rusty-brown; leaves strongly incurved-contorted (ca. 1 full turn) when dry, auriculate at the base, stem and costa dark brown to reddish; seudoparaphyllia present. 2. *A. rugelii.*

11. Plants dull-green to yellow; leaves only slightly incurved to falcate when dry, more or less decurrent, not auriculate, stem light brown, costa yellowish to light green; pseudoparaphyllia absent.

12. Leaves narrowly lingulate above constriction, this distal portion broken off; distal portion of the costa obscured by laminal cells, never bifid.

13. Secondary branching irregularly pinnate; leaves >2 mm long; costa subpercurrent; leaf apex (when leaves are intact) coarsely serrate owing to prominent whole cells. 6. *A. dentatus.*

13. Secondary branches few; leaves <1.7 mm long; costa reaching 2/3–3/4 of the lamina; leaf apex (when leaves are intact) entire. 12. *A. thraustus.*

12. Leaves constricted, but the distal portion not much narrower than the proximal one, intact; costa generally not obscured by laminal cells, sometimes shortly bifid at the end.

14. Plants robust, branches ca. 1.3 mm wide or more when dry; leaves flexuose, falcate-secund, spreading to reflexed when moist, not appressed when dry, >2 mm long. 1. *A. viticulosus.*

14. Plants of various sizes, but branches never more than 1 mm wide when dry; leaves complanate when moist, appressed when dry, <2 mm long.

15. Leaf apex rounded, margin entire; secondary branches poorly developed; inflorescences present on terminal branches, beyond the most distal branching points; leaf constriction well defined, the distal portion lingulate; secondary branches not attenuate; back of costa with large seriate papillae on each cell. 3. *A. minor.*

15. Leaf apex acute or occasionally obtuse, and almost always apiculate, often dentate; secondary branching profuse, irregularly pinnate; inflorescences never present on terminal branches beyond the most distal branching points; leaf constriction poorly defined, the distal portion tapering to triangular; apex of secondary branches attenuate; back of costa not papillose.
14. *A. attenuatus.*

I. Anomodon subgenus Anomodon.

Stems and primary branches branching in a simple pattern. Leaf apex rounded to broadly obtuse (acute to acuminate in section *Haplohymenium*); laminal cells isodiametric, hexagonal, quadrate or round in all taxa.

I.a. Anomodon section Anomodon.

Plants rather robust to somewhat slender. Secondary branches terete, never attenuate or flagelliform. Branch leaves spreading to complanate when moist, (1.2–) 1.6–4.0 (–4.8) mm long, apex not broken off (except in *A. dentatus*), obtuse to rounded; costa subpercurrent, or extending for ca. 90% the length of the leaf, not obscured by laminal cells. Sporophytes variable in size, urn >1.1 mm long (ca. 0.8 mm in *A. solovjovii*). Calyptra glabrous.

I.a.i. Anomodon subsection Anomodon.

Branch leaves broadly oblong-lingulate, constricted near the middle into a wide upper portion; apex entire, apiculate or slightly denticulate in some species; costa often shortly bifid, not obscured in its distal portion by laminal cells; laminal cells with multiple branching papillae. Seta >4 mm long.

1. Anomodon viticulosus (Hedw.) Hook. & Taylor, Muscol. Brit. 79. 1818. *Neckera viticulosa* Hedw., Spec. Musc. 209. 1801. *Hypnum viticulosum* (Hedw.) L. ex With., Syst. Arr. Brit. Pl. ed. 4, 3: 830. 1801. *Haptymenium viticulosum* (Hedw.) Fürnr., Flora 10 (2, Beil. 1): 81. 1827.—TYPE: GERMANY. Giessen, *Dillenius* (as *Neckera viticulosa* and *Hypnum viticulosum*: G-Hed.-Schwaegr. !, sine loc., c. fr., fide Grout 1932–34). Fig. 11.

Anomodon tonkinensis Besch., Bull. Soc. Bot. France, sér. 3, 41: 84. 1894.—TYPE: VIETNAM. Tonkin, Hanoi, Mt. Chua, 12–3–1888, *Bon 3789* (isotype: NY!).

Anomodon subintegerrimus Broth. & Paris, Rev. Bryol. 27: 77, 1900.—TYPE: VIETNAM. "Tonkin, inter Thai Van et Pho Lu", 18–3–1901, *Moutier* (isotypes: G! JE! NICH! NY!).

Anomodon decurrens Cardot, Bull. Soc. Bot. Genève, sér. 2, 3: 281. 1911.–SYNTYPES: JAPAN. Mitoyoshi, *J. Cardot 1190*; KOREA. Seoul, *Cardot 313* (PC).

Plants robust, forming thick mats; branches 6–8 cm long, occasionally more, and 1–1.8 mm thick when dry, erect-ascending to arcuate, stem without a central strand of differentiated cells, pseudoparaphyllia absent. Branch leaves erect when dry, secund to falcate-secund and somewhat flexuose, spreading to reflexed when moist, oblong-lingulate, abruptly narrowed below the middle from an ovate-lanceolate base, 2.2–4.0 mm long, moderately spinulose at the insertion, margins plane, tapering into an obtuse to rounded, sometimes acute apex; costa strong, pellucid, ending sharply (not obscured by laminal cells) near the apex (0.05–0.15

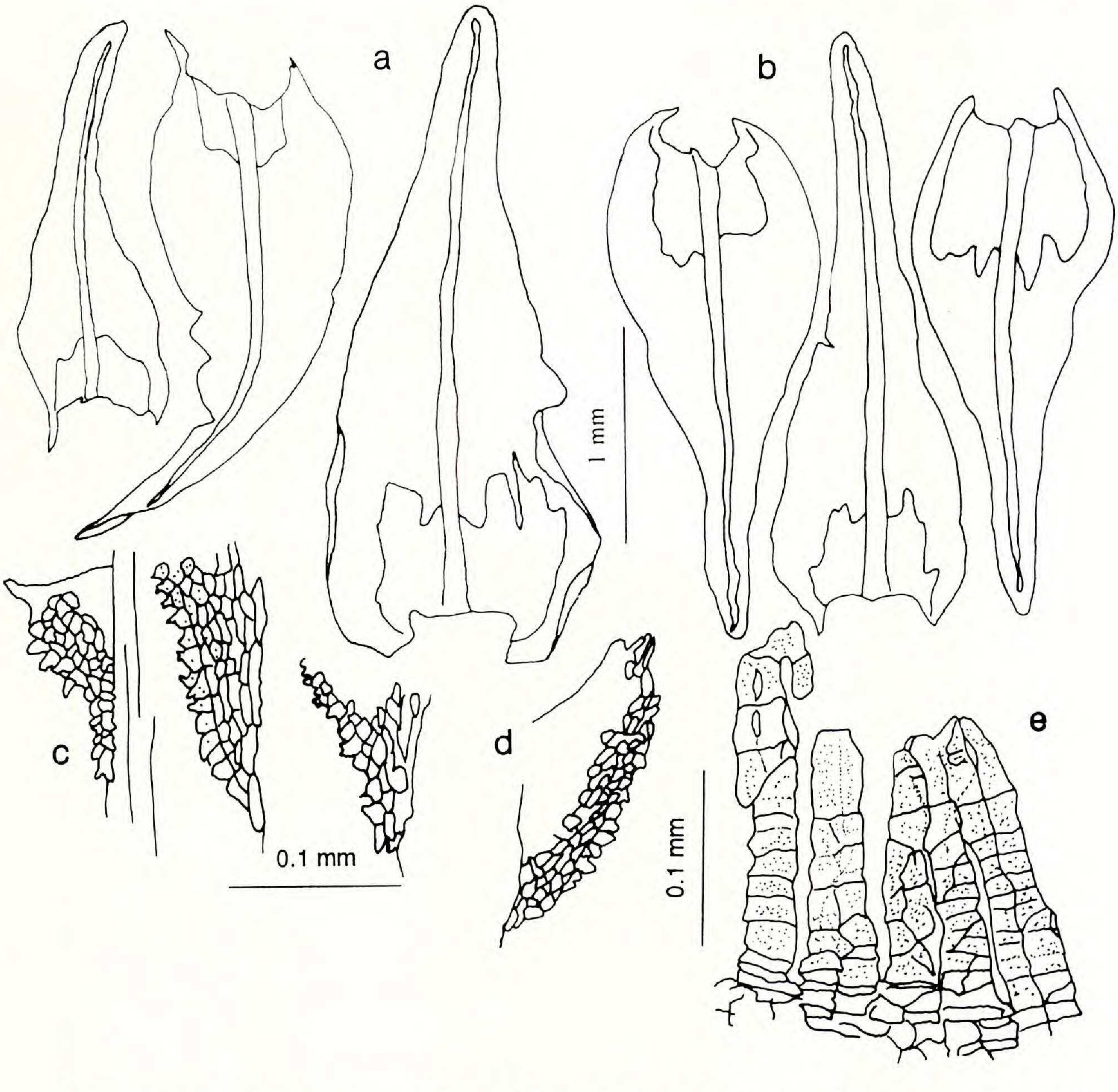


FIG. 11. *Anomodon viticulosus* (Hedw.) Hook. & Taylor. a, b, branch leaves; c, d, branch leaf insertions (showing decurrency); e, portion of peristome. Based on: a, c, e, *G.-de la Cerda 2546*, Girona, Vidrà, Rio Gés, 18–1–1988 (BCB); b, d, *Thomson 1112*, India, Simla, Oct 1849 (NY).

mm), sometimes flexuose, rarely bifid; cells at the back of the costa long, each with several thick seriate papillae; dorsal laminal cells occasionally covering the upper end of the costa, obscuring it with short cells; basal hyaline cells of the lamina barely extending beyond 1/4 the length of the leaf base, each cell bearing a single papilla, the basalmost with walls sinuose, often perforate; cells of the median lamina obscure, hexagonal, with multiple branched papillae. Inflorescences appearing distally from the most recent branching points. Perichaetial leaves, similar in shape and size to vegetative leaves, with costa ending closer to the apex, cells papillose. Seta 10–20 mm. Capsule long-elliptic, elongate, urn (1.5–) 1.8–2.8 (–3.1) mm long, stomata absent, annulus compound; operculum obliquely short-rostrate, 0.7–1 mm long; exostome 0.3–0.5 mm high, nearly smooth, with the base yellow, faintly striolate, teeth irregular, not trabeculate, with inconspicuous papillae toward the apex; endostome with basal membrane 2–4 cells (0.07–0.09 mm) high, almost smooth, segments moderately developed, 0.07–0.15 (–0.2) mm, several cells high, smooth or variably papillose. Calyptra smooth. Spores very variable in diameter between capsules, in some (19–) 20.5–23 (–25) µm, in others 15–16 µm, densely papillose. Chromosome number: n = 10 + x/y (in meiosis, Spain: Granzow-de la Cerda, 1988b).

Distribution (Figs. 12–16). *Anomodon viticulosus* is the most cosmopolitan species in the genus. Circumboreally, it occurs in North America, Asia, and Europe (where it is the most common). It has been reported from the Canary Islands by Dixon (1908) and Madeira by Luisier (1920–1922), although I have not been able to confirm these records (Granzow-de la Cerda 1988a) or others from Algeria (Düll 1985). *Anomodon viticulosus* occurs in practically all of Europe, from Spain (including the Baleric Islands) and Great Britain to Turkey, east to the Caucasus, and north to Scandinavia; in the western Himalayas from Pakistan to southern Siberia, China, Korea, Japan, Burma, and Vietnam; in eastern North America in Canada (Ontario, Québec, New Brunswick, and Nova Scotia), the northeastern United States to the southern Appalachians of Virginia and Tennessee, the Ozarks, north to Iowa; also in Mexico (Guerrero and Oaxaca). It is almost restricted to rather mesic montane calcareous environments of deciduous forests, on calcareous rocks or vertical walls, although sometimes it also occurs as an epiphyte. In Europe, *A. viticulosus* fruits frequently, but almost never in the New World or Asia, most likely because of the lack of male gametophytes in these regions. I have seen just one fruiting specimen from North America, and only one sporophyte has been reported from eastern Asia, from Japan, according to Iwatsuki (1963). *Anomodon viticulosus* is not common but locally abundant.

REPRESENTATIVE SPECIMENS. **Burma.** Pr. Now Kangi Village, *Jawahir-Singh*, 2–1–1904 (as *A. integerrimus*, NY). **China.** Hsien: Lichuan Xian, Lojiaba valley, *Exp. Sino-Amer.*, 6–10–1980 (FH). Hubei: Lichuan Xian, Lojiaba, *Sino-Amer. Exp. 1991*, 6–10–1980 (MICH, NY); Shenongjia Forest Distr., pr. Raojia, S of Shi rvr., *Exp. Sino-Amer. 1666*, 21–9–1980 (FH, MICH). Jilin: Chang Bai shan, *Lin Chang Qing 2953*, 4–1964 (IFSBH). Szechuan: Chungking, Siao lung kan, *Chen* 4–1940 (as *A. thraustus*, JE). Xishuangbanna: Mengla, Menking to I-wu, *P. Redfearn et al. 33960*, 24–12–1986 (NY). Yunnan: Songming, *pr.* Longtan, *P. Redfearn, S. He & Yi G. Su 853*, 27–7–1984 (NY). **Georgia.** Swanetia Dadianosum, *Sommier & Levier*, 29–7–1890 (FI). **India.** Himachal Pradesh: Simla, *Thomson 1112, 1116*, 10/49 (as *A. obtusifolius* Mitt., n. nud., c. fr., "type" in herb. Mitten NY); Kangra, Kulu, *Koeltz 7510*, 24/27–11–1933 (c. fr., DUKE, MICH). Maharashtra: Bombay, Rachira, *Marchal*, 5–1869 (c. fr., FI). Punjab: Murree, *Stewart*, 9–1948 (NY). Uttar Pradesh: Tihri Garwal, Kidarkanta, *Bahadru*, 12–6–1904 (as *A. integerrimus, c. fr.*, NY); Musoorie, Dhanoutti, *Bahadru*, 10–12–1903 (as *A. integerrimus*, NY). **IRAN.** Mazanderan, 30 km S of Amal, *P. Goldblatt 1221a*, May 1973 (FH, MO). **Japan** (as *A. decurrens*). Hondo: Akiyoshi, Nagato, *S. Matsumoto*, Mar 1932 (NICH). Honshu: Jaisaku pref., Bingo, *A. Noguchi*, 7–7–1934 (NICH); Okayama pref., Niimi-shi, *A. Noguchi* 3–11–1954 (NICH); Shiga pref., Sakata-gun, Kaminyû, *T. Nakajima*, 4–4–1978 (MICH). Kyushu: Fukuoka pref., Hisaodai, *T. Osada*, 2–5–1955 (MICH), Kaharu Mt., *A. Noguchi*, 13–9–1953 (NY), Kawaradake, *A. Noguchi*, Sep 1953 (MICH); Kumamoto pref., Kuma-gun, Koonose, *Takaki 2302*, 11–8–1946 (NY), *K. Mayebara*, Dec. 1947 (MICH), Itsuki-mura, Sangaura, *A. Noguchi & Imae*, 23–4–1956 (NICH); Oita pref., Kuwanobori-mura, *A. Noguchi*, 23–11–1953 (NICH); "center of back bone, Mt. Kumimi," *Kuwahara 2180*, 12–8–1951 (NY). **Nepal.** Longtang Himal: Dunche to Kyangjing, Langtang Khola, *W. Weber B–99386*, 21–10–1991 (NY). **Russia.** Gorno-Altaisk: SE of Ust-Syana, Katun rvr., *T. Elias et al. B–65178, 65180*, 17–8–1978 (NY). **Taiwan.** Tienhsiang, Tailuko rvr., *Z. Iwatsuki & A. Sharp 1787*, 27–3–1965 (FH). **Thailand.** Phu khieo, E of Chaiyapun, *Lorsen, Nielsen & Santisuk 31305*, 3–8–1972 (NY). **Turkey.** Trabzon: Maçka, Pontus Mts., *Godfrey 728*, 24–9–1952 (NY).

Canada. Nova Scotia: Cumberland Co., Wentworth, *R. Ireland 10673*, 7–9–1967 (as *A. minor*, DUKE). Ontario: Bruce Co., 2 km N of Colpoys Bay, *R. Ireland 20290*, 12–7–1982 (MICH), White Bluff, *R. Ireland 20396*, 14–7–1982 (FH); Grey Co., Inglis Falls, *H. Crum 11008*, 3–8–1961 (DUKE, MICH), Jones Falls, *R. Ireland 20198*, 11–7–1982 (FH); Lincoln Co., betw. Vineland and Beamsville, *H. Crum 31, 42*, 5/7–10–1964 (MICH); Ottawa, *Bauer*, 31–3–1902 (FH). Québec: Gatineau Co., King Mt, Gatineau Park, *R. Ireland 15853*, 27–4–1972 (MICH); Hull, *J. Macoun*, 22–4–1896, 18–5–1901 (MICH). **Mexico.** Guerrero: Omiltemi, 30 km W of Chilpancingo, *A. Sharp 1118c, 1122*, 27–10–1944 (as *A. minor*, MEXU, MICH). Oaxaca: S. Pablo Ayutla, 70 km E of Oaxaca, *A. Sharp et al.*, 23–12–1972 (MEXU). **U.S.A.** Arkansas: Newton Co., junc. Leatherhood Creek and Buffalo Rvr., *P. Redfearn 29261*, 2–2–1972 (MICH). Michigan: Alpena Co., SW of Posen, Leer Road, *Düll 1152/3*, 18–8–1981 (MICH); Delta Co., Burnt Bluff, *H. Gleason 2390*, 22–8–1939 (MICH), *W. Steere 760*, Aug. 1934

(FH); Keweenaw Co., gorge of Manganese Rvr., *W. Steere*, 1–9–1936 (MICH); Mackinac Isl., *E. & S. Harper*, 18–7–1899 (MICH), *I. Schnooberger 2749*, 21–7–1939 (MICH); Presque Isle Co., nr. Long Rapids, *R. Fidler 89*, 3–8–1974 (MICH). Minnesota: Winona, *Holzinger*, 1890 (FH). New York: Buffalo, *G. Clinton* (MICH), Niagara Falls (ex Sullivant & Lesqureaux, MICH); Clinton Co., Ausable Chasm, *L. Anderson 20608*, 5–9–1968 (DUKE, MICH). Vermont: Glebe Mtn., Newfane, *A. Grout*, Aug. 1900 (as *A. viticulosus* var. *microphyllus*, FH). Virginia: Marion, *A. Vail & E. Britton*, 23–5–1892 (MICH); Giles Co., *E. Byers 16*, 4–7–1949 (MICH), Newport, *I. G.-de la Cerda 1892, 1898*, 7–10–1892 (DUKE). Tennessee: Anderson Co., Savage Gardens, *A. Sharp*, 13–1–1957 (MICH, TENN), *I. G.-de la Cerda 1906 & A. Sharp*, 8–10–1984 (DUKE).

Austria. Salzburg, pr. Fürntenstein, *J. Zimmerman*, 6–5–1868 (c. fr., FH); "Traunfall, pr. Schwanenstadt," *Matouschek* (c. fr., FH, FI); Bergwälder, *Klaus*, Jul 1910 ("var. *latifolius*," c. fr., NY). Tirol: Windish Matrai, Klamm, *E. Bauer 1217*, Aug 1911 (MICH); Innsbruck Sillschlucht, *Luisier* 22–3–1904 (c. fr., INA). **Belgium.** Auderg hem, *Piré* (c. fr., FI); betw. Rochehaut & Ucimont, *J.L. De Sloover 16439*, 1–7–1973 (MICH); Louvaine, pr. Tournay, *Marissal*, (c. fr., FH); Orval, *J. Cardot* (FH). **Croatia.** Istra, above Icici, pr. Opatija, *J.P. Frahm 10034*, 26–3–1975 (c. fr., MICH). **Czech Republic.** Bohemia: "Karlstein," *Bauer*, 24–4–1890 (c. fr., FH). "Mähr-Weisskirchen," Surkow, *F. Petrak*, 9–4–1913 (FH). **Denmark.** Mariager kridtbrud, *K. Holmen & E. Warncke 237* (MICH); Möen, Klinteskoven, *H. Möller*, 1/3–6–1893 (c. fr., FH). Sjœland: Farum, Nørreskov, *G. Smith*, 24–10–1967 (FH); Sorö, Suserup, *F. Hermann 15885*, 28–5–1960 (MICH). **Finland.** Tohmajärvi, Kb: Havukkavaara, S of Vuorenpää, *R. Fagerstén & M. Haapassari 4097 dup.*, 2–10–1984 (FH, MICH); Rükola, *R. Fagerstén & M. Hapasaari 4120*, 3–10–1984 (FH). "Karelia borealis," Juuka, Polvijärvi, *A. Huuskonen*, 19–8–1965 (FH). **France.** Ariège: Bagnères de Luchon, *C. Casas*, 20–9–1956 (BCB). Basses-Pyrenés: St. Etienne-de-Baigorry, *M. Fleischer*, 10–5–1908 (FH). Calvados: Pont des Vers, *Husnot*, (c. fr., FH). Gard: Méjanes-Le-Clap, *J. L. De Sloover 44850*, 12–7–1988 (MICH). Haute-Savoie: Salève, Archenes, *R. Blanche*, 15–2–1954 (c. fr., MICH). Isère: Bains-la-Romaine, *J. L. De Sloover 34593* 10–7–1981 (MICH). Savoie: Saint Claude, "prés de Chambèri," *Songeon*, 20–10–1866 (c. fr., FI). **Germany.** Giessen, *Wanschoff*, (c. fr., FH); München, Dodel-Port., 20–2–1869 (c. fr., FH); "Rhinefall," *Mann & Cummings*, 4–3–1887 (c. fr., FH). **Greece.** Ioannina: Epirus, pr. Emin Agha, *K. Rechinger*, 12–5–1961 (MA). Thessalia: Lutropigi, Smokovo, *K. Rechinger*, 8–5–1961 (MA). **Ireland.** Sligo: Knocknarea, *H. Conrad*, 4–8–1935 (FH). **Italy.** Caiagilo, pr. Varesse, *E. Corti*, Mar. 1905 (c. fr., FH). Lavione: "pr. Florentiam," *J. Arcangeli*, 23–12–1877, (c. fr., FH). Lombardia: Parco di Monza, *Mazzucchelli*, 19–9–1878 (c. fr., FI); Piemonte: Campello-Monti, Roncaccio, *Levier*, 30–7–1906 (FI); Como, Torno, Lago di Como, *Artaria*, 2–1902 (FH). San Marino: Borgo, Ornella, *Pampanini*, 8–1–1916 (c. fr., FI). Trento: Lago Tadel, Serra del Lago, *Cortini 973*, 16–7–1958 (FI). Venezia: Padova, *Fiori*, 23–4–1893 (c. fr., FI). **Macedonian Republic.** W of Tetoro, Popova Sapka., exp. Rheno-Trai *68–1526*, 10–7–1968 (MEXU). **Norway.** Södra Trondheim, Håkån, *J. Hagen*, Jul 1899 (MICH); Lysaker, pr. Oslo, *I. Hagen 18–10* (FH). **Poland.** Krosno: Kurników Beskid, *R. Ochyra*, 7–7–1977 (BCB, MICH); Nowy Sacz, Spiskie Klippen (W. Carpathians); Zielone Skaly, Dunajec rvr., *R. Ochyra 657*, 1–6–1979 (BCB, MICH); Kramnika Klippe, Rvr. Bialka, *R. Ochyra 564*, 19–6–1979 (MICH). Skata Knity (Krakov): Zabiezowic, *Z. Zmuda*, 22–4–1911 (FH). **Russia.** Moscow, "Wald von Kunzowo," *Heyden*, 1–8–1900 (FH). **Slovakia.** Gau Kaschau, Snina, Vinicna hora, *Bauer*, 31–7–1925 (FH); Tatra Magna, Tscheckengrund valley, *I. Györffy 42*, 6–8–1927 (MICH). **Spain.** Barcelona: Montserrat, Sant Geroni, *C. Casas*, 5–10–1947 (BCB). Cantabria: Puente Viesgo, *A. Casares* Aug. 1911 (MA). Castelló: Mangraner, La Cénia, barranc de la Fou, *C. Sérgio et al. 4.1*, 14–2–1984. Girona: Sta. Maria de Besora, Serra de Caraups, *I. G.-de la Cerda 2554* 18–1–1988 (BCB). Vidrà, rio Ges, rec de l'Espirau, *I. G.-de la Cerda 2316, 2322 & M. Sanz*, 10–1–1987, *I. G.-de la Cerda 2546*, 18–1–1988 (c. fr., BCB). León: Posada de Valdeón, Garganta del río Cares, *I.G.-de la Cerda*, 1–1–1990 (BCB). Lleida: Pallars Sobirà, "entre Rialp i Llesui," *C. Casas* 6–10–1981 (BCB). Lugo: Lózara, *F. Merino* (c. fr., INA, herb. Luisier). Navarra: Alto de Lizarrusti, *A. de Miguel & A. Ederra*, 27–11–1983 (c. fr., NAU). (see Granzow-de la Cerda 1988a). **Sweden.** Jämtland: Brunflo, Backen, *C. Stenholm*, 31–7–1934 (MICH). Öland: Borgholm, *E. Ekstrand*, 8–7–1975 (c. fr., MICH), *H. Möller*, 16–4–1908 (FH). Skåne: Kårgeröd, Ylmesåken, *C. Stenholm*, 25–5–1934 (FH). Uppsala: Gottsunda, S of Fäbodarna, *F. Österlind*, 3–5–1951 (FH, MICH). **Switzerland.** "Switzerland" ? (DUKE). Mt. Salève, *M. MacFarlane*, Feb 1911 (c. fr., FH). Splügen, *Areschoug*, Jun 1861 (c. fr., FH). Genève: Chatelaine, *Boissier*, Mar.1821, (c. fr., MICH). Zürich, *P. Culmann*, 11–3–1880 (c. fr., FH). **United Kingdom.** Scotland: *W. Wilson*, 320 9–7–1861 (c. fr., FH). Anglesey [Gwynedd]: Tyfry, *W. Wilson*, Mar. 1830 (c. fr., MICH). Devon: Honiton, *H. Shacklette 2266* 25–1–1943 (MICH), Plymouth, *Holmes*, 1867 (c. fr., FI). Gloucester: Lead, Morgan's wood, *E. Elliot*, 18–1–1886 (c. fr., FH). Somerset: Weston-Super-Mare, 2km NNW Chedar, *Jury et al. J1787*, 8–1–1983 (BCB). Wiltshire: Edington, pr. Bridgenorth, Morl Brook, *I. G.-de la Cerda 2018*, Jul 1884 (DUKE).

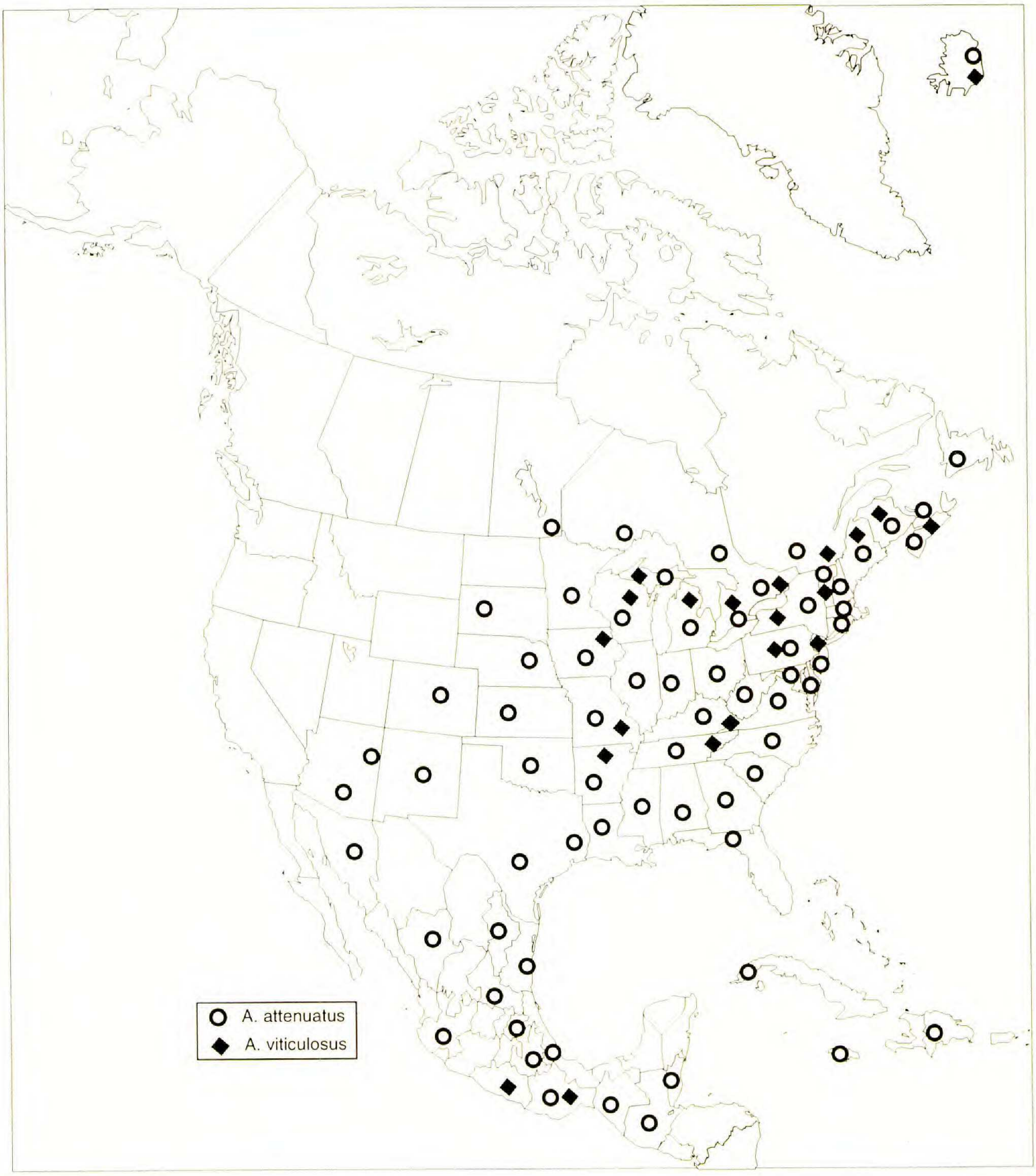


FIG. 12. Distribution of *Anomodon attenuatus* and *A. viticulosus* in the New World.

Anomodon viticulosus is the most robust species of the genus. It forms thick mats on rocks and sometimes also on tree trunks. The robust habit and the thickness of the mats make it clearly distinguishable from any other species for which it could be mistaken, such as *A. attenuatus*, *A. rugelii*, or *A. minor*. In depauperate populations of *A. viticulosus*, this species can be distinguished from *A. rugelii* by its decurrent instead of auriculate leaves. Also, *A. rugelii* has incurved leaves when dry, whereas those of *A. viticulosus* are, at most, falcate-secund, tapering toward the apices from the shoulders. The apex is never rounded, as in *A. rugelii*, *A. minor*, and *A. thraustus*. The branches are not complanate, as in *A. rugelii* or *A. minor*. The latter species forms much looser mats than *A. viticulosus*. The endostomes of *A. minor* and *A. viticulosus* differ considerably; they are rudimentary in *A. minor* and better developed in *A. viticulosus*. Some specimens, however, have a very rounded leaf apex, therefore resembling *A. minor* (most often seen in specimens from

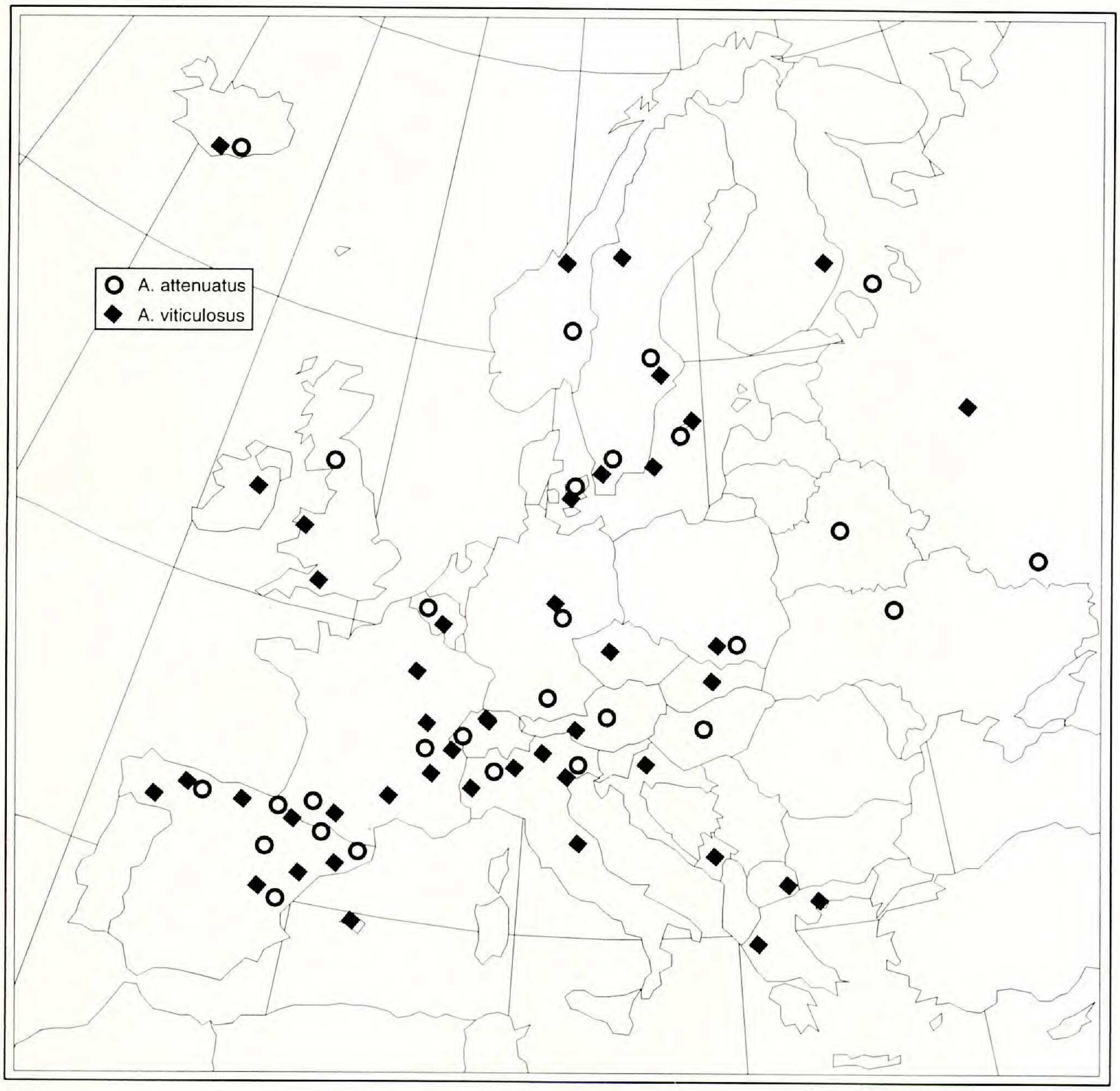


FIG. 13. Distribution of *Anomodon attenuatus* and *A. viticulosus* in Europe.

central Mexico). *Anomodon viticulosus* is sometimes mistaken for *A. attenuatus*, although this species has more prostrate stems and its branching pattern is different, mostly more profuse. Branching in *A. attenuatus* occurs in several successive orders; the terminal branches are attenuate, complanate, crowded and somewhat fasciculate. In *A. attenuatus* the back of the costa is smooth, and perichaetia do not develop on the last year's branches (but only in older portions of branches).

Most specimens of *A. viticulosus* from Japan have been called *A. decurrens*. It is true that some specimens from these islands may have slightly more slender leaves. Also, some individuals – within the same specimen along with typical forms of *A. viticulosus* – may resemble either *A. attenuatus* or *A. minor* in habit. Nonetheless, there are no differences to account for placement of such plants in any taxon other than *A. viticulosus*. *Anomodon dentatus*, a rare endemic from northeastern China, is a more delicate plant, although similar in habit to *A. viticulosus*; also, the portion of the leaves above the shoulder in *A. dentatus* is lingulate to slightly spatulate, with a serrate apex, often broken off. *Anomodon tonkinensis* and *A. subintegerrimus* are examples of depauperate forms of *A. viticulosus*, with less crowded leaves (perhaps somewhat reminding of *A. minor*), which do not deserve taxonomic consideration.

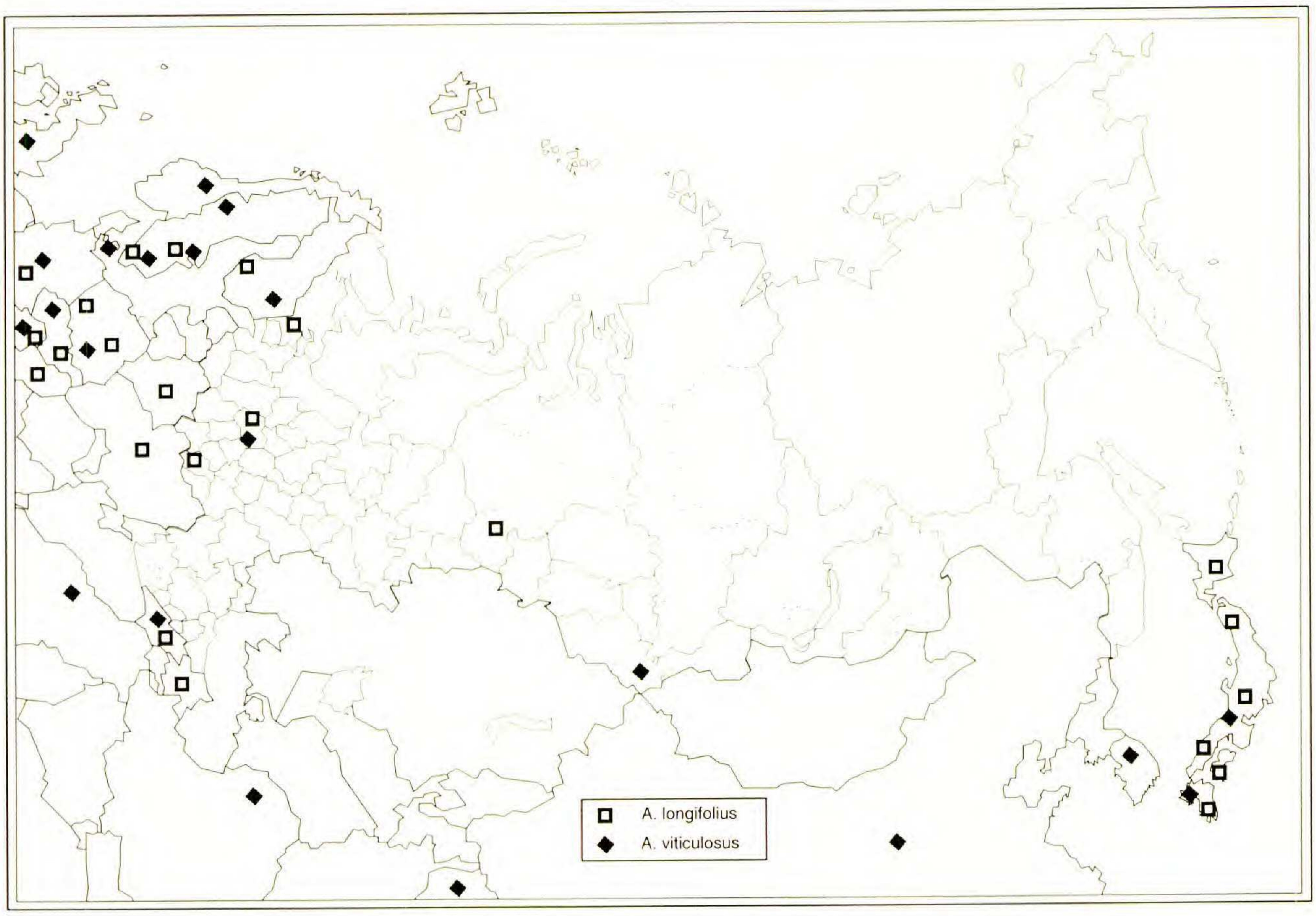


FIG. 14. Distribution of *Anomodon longifolius* and *A. viticulosus* in northern Eurasia.

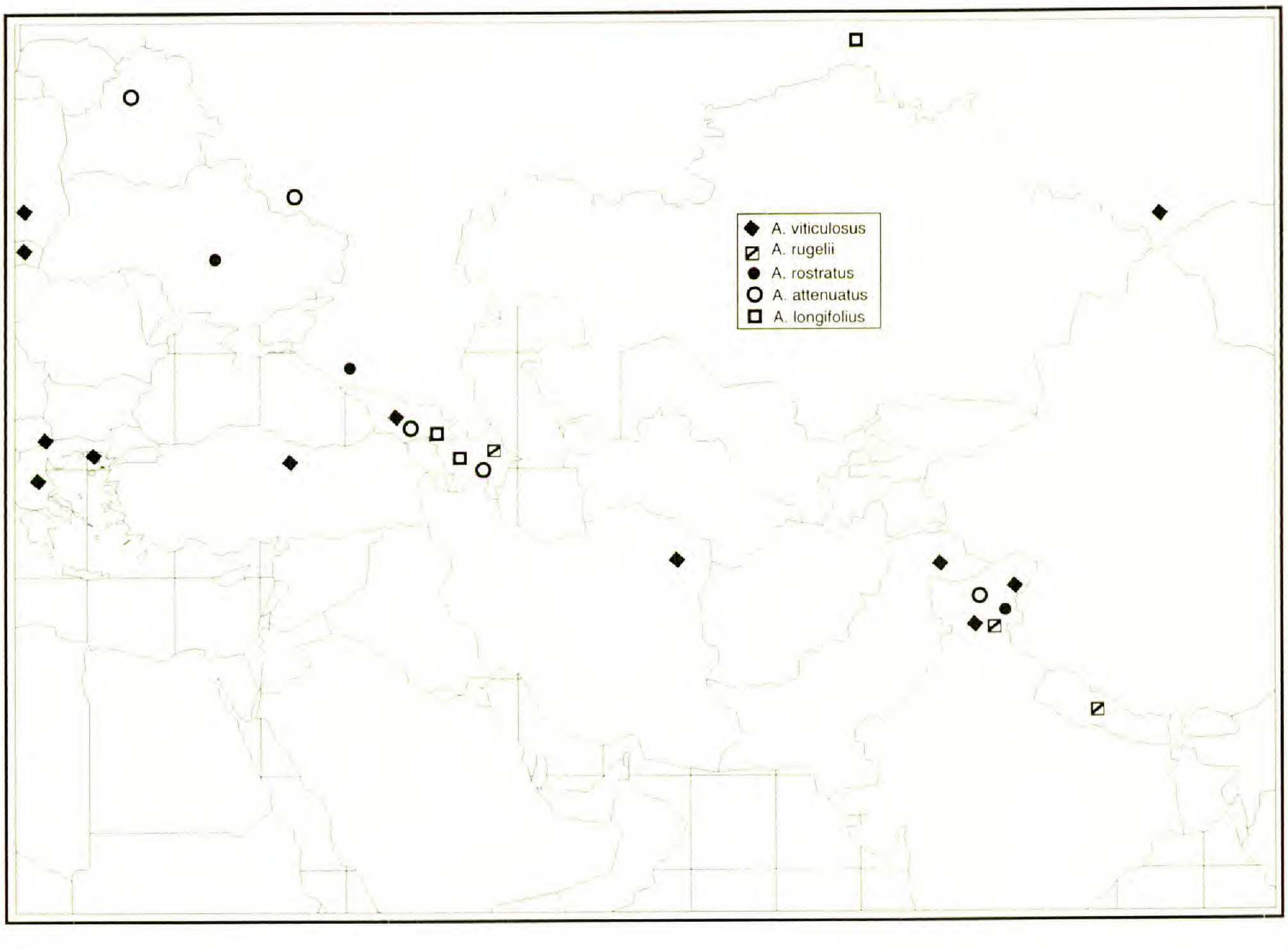


FIG. 15. Distribution of *Anomodon attenuatus*, *A. longifolius*, *A. rostratus*, *A. rugelii*, and *A. viticulosus* in eastern Europe and central Asia.

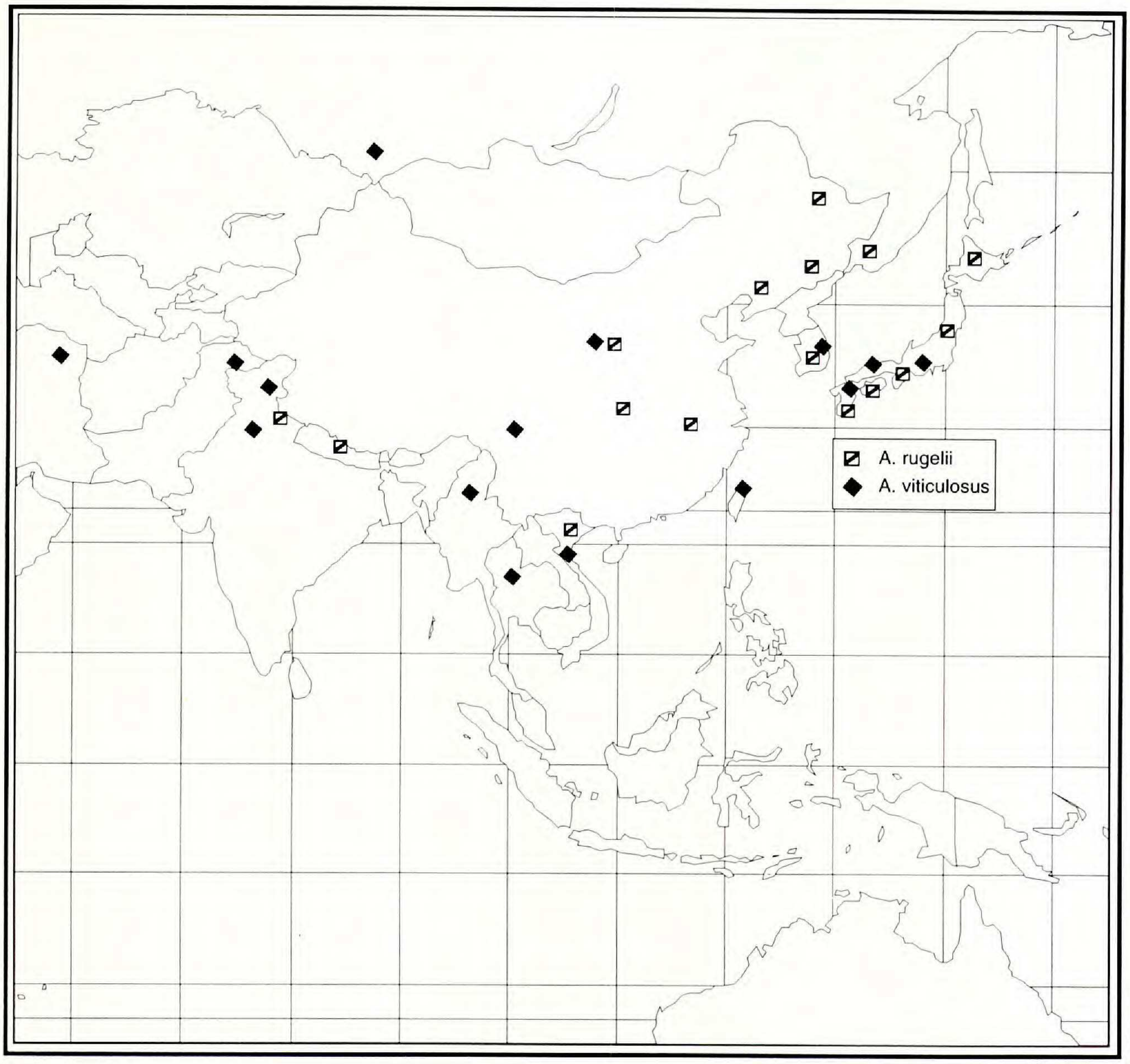


FIG. 16. Distribution of *Anomodon rugelii* and *A. viticulosus* in central and eastern Asia.

Anomodon viticulosus is the type species for*Anomodon* Hook. & Taylor (1818; basionym: *Neckera viticulosa* Hedw.) The original material on which Hedwig based his description was Linnaeus's "*Hypnum viticulosum*," collected by Dillenius near Giessen in Germany (Grout 1934).

2. Anomodon rugelii (Müll. Hal.) Keissl., Ann. Naturh. Hofmus. Wien 15: 214. 1900. *Hypnum rugelii* Müll. Hal., Syn. 2: 472. 1851.—Type: U.S.A. Tennessee, Smoky Mountains, *Rugel s.n.* (holotype: not located). Fig. 17a, b.

Anoectangium ferrugineum Besch., Ann. Sci. Nat. Bot. 17: 329. 1893. *Anomodon ferrugineus* (Besch.) Nog., J. Jap. Bot. 20: 260. 1944. *Anomodon rugelii* var. *ferrugineus* (Besch.) Z. Iwats., J. Hattori Bot. Lab. 26: 51. 1963.—Type: Japan. Yezo, montagnes d'Yesashi, 6–6–1889, *Faurie 3543* (FI?).

Anomodon uyematsui Broth., Bull. Soc. Bot. Genève, sér. 2, 3: 281 1911. *Anomodon uematsui* Broth., Öfver. Finsk. Vet. Soc. Förh. 62: 33. 1919–1920.—Type: Japan. Hokkaido, Iwate pref., Rikuchu Nat. Park, Mt. Hayachine, 27–7–1906, *Uematsu 3390* (isotype?: NY!).

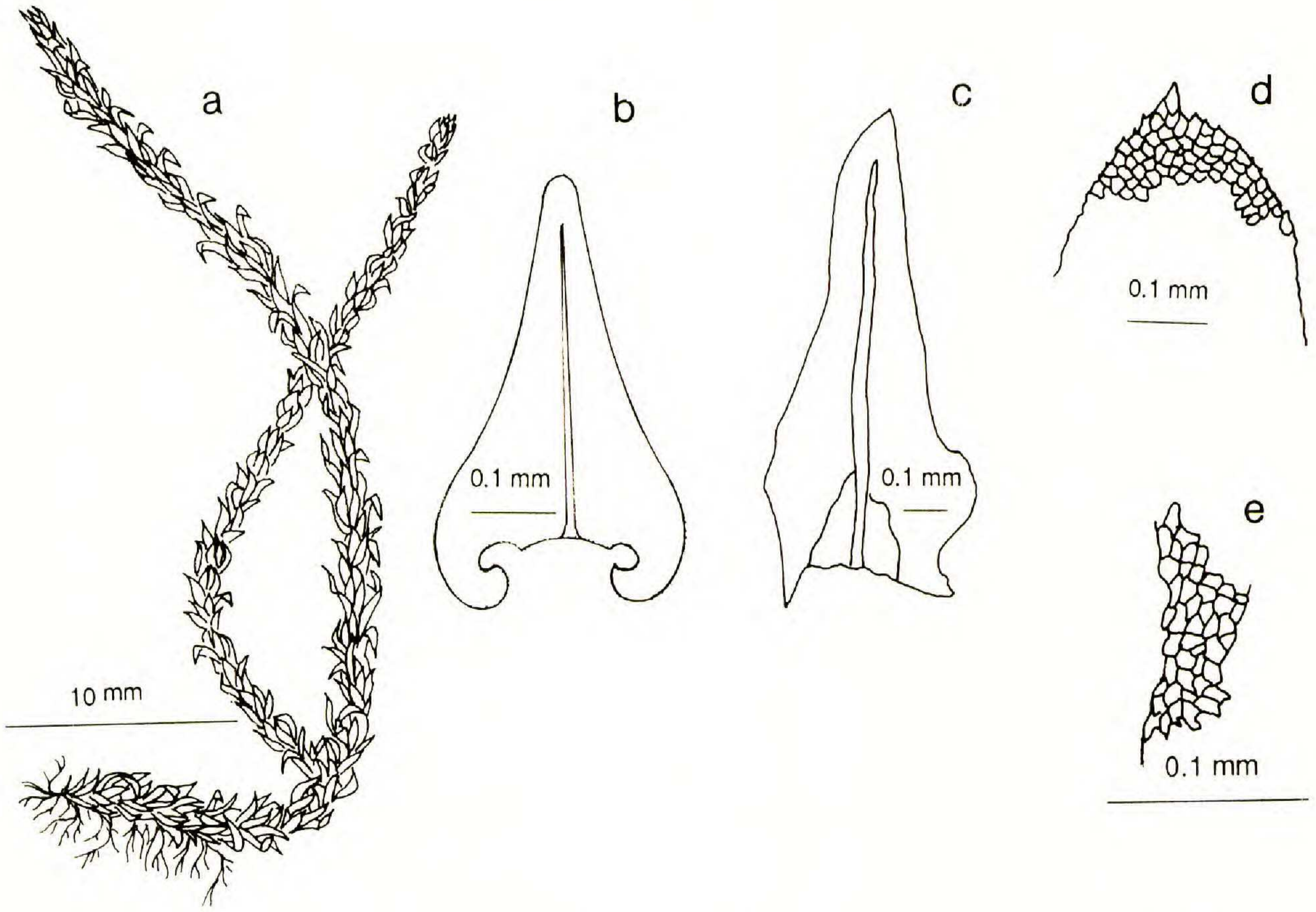


FIG. 17. *Anomodon rugelii* (Müll. Hal.) Keissl. and *A. attenuatus*. (Hedw.) Hüb. a, b, *A. rugelii*. a, branch leaves; b, stylized representation of a branch leaf. c–e, *A. attenuatus*. c, branch leaf; d, leaf apex; e, leaf insertion. Based on: a, b, *G-de la Cerda 2512 & Renzaglia*, USA, North Carolina, Joyce Kilmer Mem. Park, 3–10–1987 (DUKE, MA); c–e, *Standley*, Guatemala, Alta Verapaz, Río Carché, 12–4–1941 (NY).

Plants rather slender, forming thick, dense mats, dark green to rusty-brown. Stems and main branches to 3.5 (–5) cm long, 0.8–1.5 mm thick when dry, creeping, with few primary branches, erect-ascending, somewhat arcuate, poorly branched, dark reddish brown, without a central strand, with foliose, often narrow to uniseriate, golden-yellow pseudoparaphyllia, generally with abundant rhizoids. Branch leaves incurved-contorted (ca. 1 full turn) when dry, erect-spreading, somewhat secund when moist, (1.2–) 1.4–2.3 (–2.5) mm long, broadly oblong-lingulate from an ovate, auriculate base; margins of auricles strongly spinulose, with high and branched papillae; apex broadly obtuse to rounded, often apiculate; costa strong, pellucid, golden-yellow to rusty-brown, ending sharply near the apex, generally bifid, sometimes slightly flexuose at the end; cells of the costa elongate, smooth on the back, up to 70 µm long; basal cells hyaline and well differentiated, occupying more than half the basal portion of the lamina, their walls not papillose, somewhat irregular, often sinuose; medial laminal cells hexagonal, 7–12 µm long, with multiple high and branched papillae; marginal cells of the auricles with 1–2 strong branched spinelike papillae, occasionally minutely denticulate at the apex. Perigonia and perichaetia at the end of terminal secondary branches. Perigonial leaves with few or no papillae, upper margins crenulate. Perichaetial leaves abruptly narrowed toward the apex, becoming almost subulate, cells papillose. Seta length variable, (5–) 9–22 mm. Urn (1.2–) 1.8–2.3 (–2.5) mm long, elongate, with stomata at the base; annulus absent, operculum conic to obliquely short-rostrate, 0.5–0.8 mm long; exostome 0.15–0.30 mm high, teeth regular, papillose throughout, often inconspicuously horizontally striolate at the base, trabeculate above; endostome rudimentary, 0.042–0.057 mm high, with a basal membrane 2–4 (–6) cells high, segments very reduced (1 cell high) or absent. Calyptra smooth. Spores 9.5–14 µm in diameter, slightly papillose. Chromosome number: n = 10 + x/y (in meiosis, North Carolina: Granzow-de la Cerda, 1988b).

Distribution (Figs. 15, 16, 18, 19). Present in Asia, eastern North America and Central Europe; circumboreal montane, growing in deciduous forests. *Anomodon rugelii* forms extensive, dense and thick mats on tree trunks, generally, although not always, 1–2 m above the base. Some specimens have been collected from both basic and acidic rocks. Sporophytes are found in fair abundance.

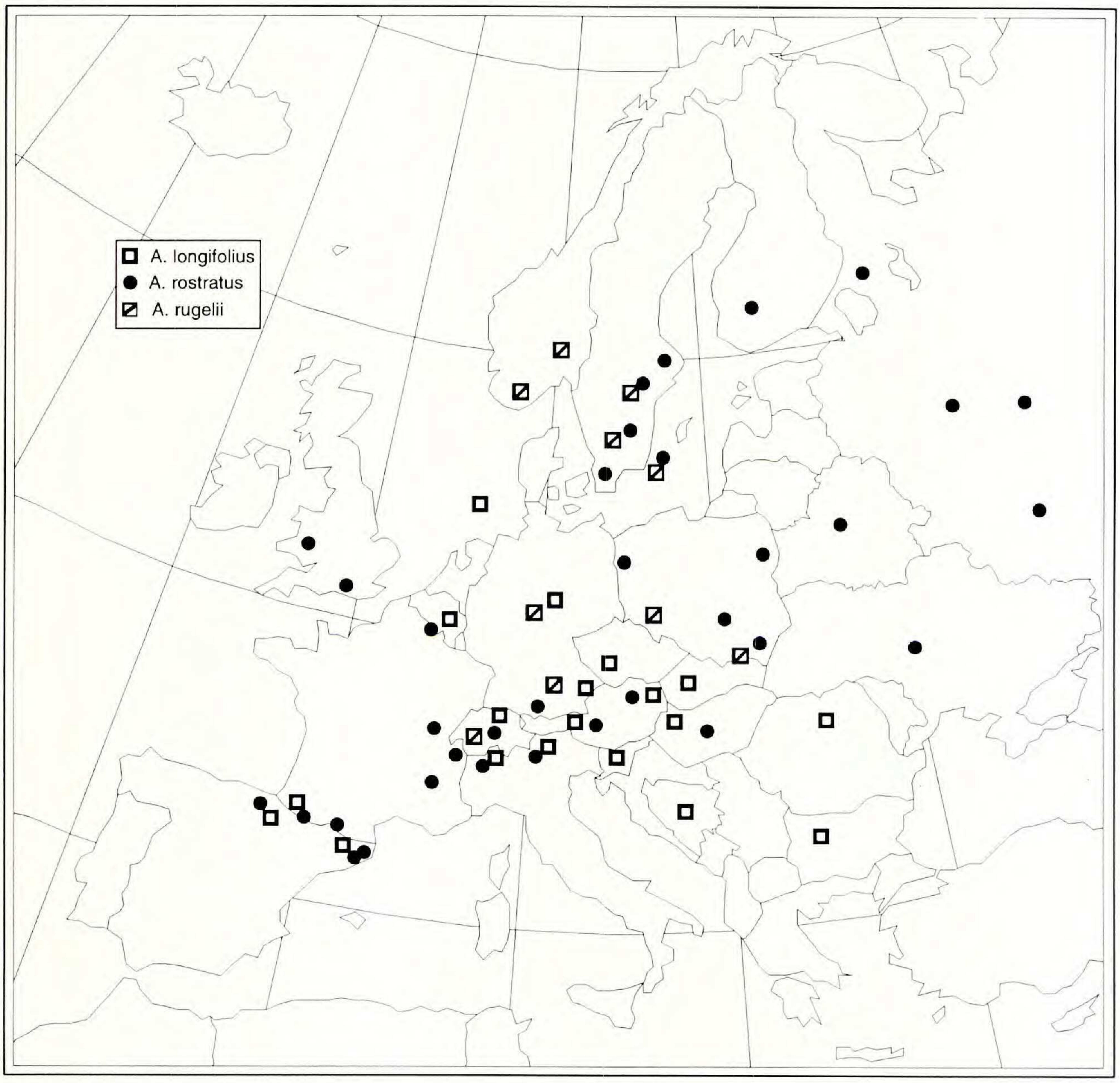


FIG. 18. Distribution of *Anomodon longifolius*, *A. rostratus*, and *A. rugelii* in Europe.

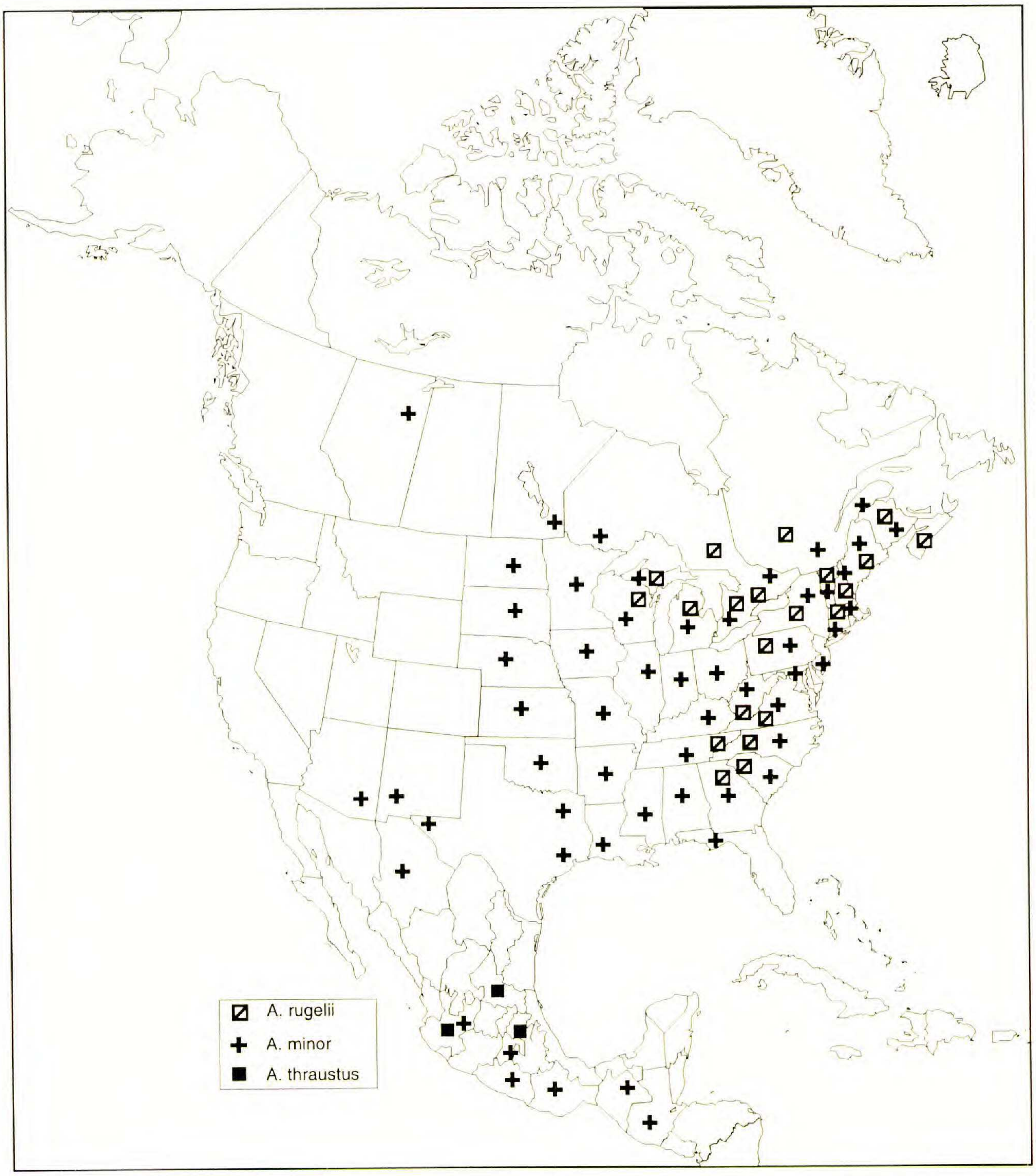


FIG. 19. Distribution of *Anomodon minor, A. rugelii,* and *A. thraustus* in the New World.

Representative Specimens. **Azerbaijan.** Bakuriani, *A. Lazarenko & Abramov*, 17–9–1956 (NY). **China.** Hubei: Shennongjia Forest Distr., "from Quiujiajing to Laojun," *Sino-Amer. Exp. 655c*, 3–9–1980 (NY). Jilin: Chang Bai shan, *Guo Qian 22137*, 24–9–1981 (NY). Liaoning: "Ansha, monte Chien," *Chen Gao 1889*, 19–8–1958 (as *A. ferrugineus*, IFSBH). Heilongjian: distr. Hailin, Dahai, Laotudingzi shan, *Guo Qian 9147*, 28–8–1973 (IFSBH). **India.** "Tonglo top 10000" (as *A. planatus*, "syntype" p.p., ex herb. Mitten NY). Uttar Pradesh: Tehri Garwal, Kidarkanta, *Bahadru*, May 1904 (NY), *Gollan*, 23–5–1904 (c. fr., FH, NY). "India orientalis": *Bell 367* (as *A. minor*, ex herb. Mitten NY). **Japan.** Hokkaido: Sapporo, Mt. Moiwa, *N. Iwasaki*, 17–11–1913 (c. fr., NY). Honshu: Nantaizan, *Bisset* (as *A. ramulosus*, syntype, p.p., NY); Aomori pref., Arase, *A. Noguchi*, 1–9–1954 (as *A. ferrugineus*, NICH); Etigo, Sekida-toge (Seki), *Z. Iwatsuki 3390*, 21–8–1935 (as *A. uematsui*, NY); Kyoto pref., Kita-Kuwade-gun, Sasari-toge, *T. Nakazima 5553*, 2–5–1954 (as *A. ferrugineus*, NICH); Mie pref., Hirakura forest, *T. Nakajima 11940*, 6–5–1961 (as *A. ferrugineus*, NICH); Nagano pref., Aumo-mura, *Mizushimako*, 28–9–1954 (c. fr., NY), Kami-ina-gun, Akagawara, *Takaki*, 5–8–1933 (c. fr., NY), *Nakajima*, 22–8–1973 (NY); Nara pref., Yoshimo-gun, Nosegawa-mura, *T. Nakazima 8708*, 3–5–1958 (as *A. ferrugineus*, NICH), Mt. Odaigahara, *T. Nakazima 1907*, 16–10–1948 (as *A. ferrugineus*, NICH); Okayama pref., Maniwa-gun, Mt. Kani-hirsen, *C. Igi 5812*, 12–11–1957 (c. fr., as

A. ferrugineus, NICH); Saitama pref., Chichibu, Higashi-dani, *I. Nagano 546*, 4–11–1951 (as *A. uyematsui*, NICH); Tottori pref., Yazu-gun, Mt. Nagi-sen, *H. Ochi 1582*, 26–8–1951 (as *A. ferrugineus*, NICH); Toyama pref., Mt. Tateyama, *Z. Iwatsuki*, 13–8–1955 (NY); Kurabe, Keyakidaira, *A. Noguchi*, 13–10–1953 (as *A. ferrugineus*, NICH); Komagataka, *Faurie 3493*, 1905 (c. fr., NY). Kyushu: Oita pref., Mts. Kuju, Kurodake, *M. Miyamoto 2431*, Jul 1960 (c. fr., as *A. ferrugineus*, NICH). **Nepal.** E. Himalaya: Kathmandu, Mt. Phulchoki, *Z. Iwatsuki 2470*, 15–7–1972 (NY). **Russia.** Reg. austro-ussuriensis, "fontem flumen Ssputinka," *A. Lazarenko*, Oct 1934 (NY).

Canada. New Brunswick: Grand Falls, *H. Habeeb* 86, 1–11–1945 (NY), Aroostook Falls, *J. Collins 2770*, 17–7–1902 (MICH). Victoria Co., Kilburn, *R. Ireland 12758*, 9–7–1970 (MICH). Nova Scotia: Digbi Co., Acaciaville, *R. Ireland 17890*, 28–7–1974 (MICH, NY). Ontario: Carleton Co., Fallowfield, *H. Crum 290*, 28–10–1964 (MICH). Huntsville Co., Muskoka Distr, NW of Chaffey Twp., *R. Ireland 22021*, 23–7–1986 (MICH). Algonquin Park, *J. Macoun*, 8–6–1900 (MICH). Manintulin Distr., Sheguindah, Howland Twp., *R. Ireland* 22372, 30–7–1987 (NY). Muskoka Distr., Moon rvr., Medora Twp. (Foots Bay), *R. Ireland 24032*, 7–9–1982 (NY). Québec: Terrebonne Co., E of Mt. Tremblant Lodge, *H. Crum 9885*, 23–8–1958 (MICH); Gattienau, nr. Kingsmere and Old Chelsea, *H. Crum 2468*, 1954 (NY); St. Hyacinthe, *F. & M. Anselme A-5*, 3–5–1948 (NY). Pontiac Co., Park de la Vérendrye, Lac Serpent, *R. Ireland 15969 & T. Koponen*, 13–6–1972 (NY). **U.S.A.** Maine: Pleasant Ridge, Bean Pond Ridge, *J. Collins 2455*, 21–7–1901 (as *A. viticulosus*, MICH). Michigan: Keweenaw Co., "on ledge at Delaware," *W. Steere*, Sep 1936 (as *A. viticulosus*, FH). New York: Cayuga Lake Basin, *Dudley*, 16–5–1884 (c. fr., DUKE); Lake Placid, *Britton*, 9–8–1898 (DUKE); Adirondack, Essex Co., North Elba, *Hermann 14776*, 10–8–1958 (DUKE); Catskills, St. Lawrence Co., Cranberry Lake, *N. Slack 2031*, 25–6–1976 (DUKE). North Carolina: Roan Mountain, *Weatherby*, 24–2–1894 (as *A. minor*, c. fr., DUKE); Graham Co., Joyce Kilmer Mem. Park, *I. G.-de la Cerda & K. Renzaglia*, 3–10–1987 (c. fr., DUKE, BCB); Macon Co., Chatooga river, *I. G.-de la Cerda 1454*, 1–7–1984 (DUKE); McDowell Co., Linville Falls, *I. G.-de la Cerda 1931*, 21–10–1984 (DUKE); Watauga Co., Sim's Creek, Blowing Rock, *L. Anderson*, 27–9–1984 (c. fr., DUKE); Yancey Co., Crabtree meadows, *I. G.-de la Cerda 1925*, 20–10–1984 (DUKE). Pennsylvania: McKean Co., Bennet Brook, *Burnett 2831*, 7–11–1897 (FH). Vermont: Willoughby, Humphry Brook, *Kennedy*, 27–10–1897 (as *A. obtusifolius*, FH).

Germany. Bayern: Allgäu, "Sauwald ober Hinterstein," *Holler*, 22–8–1892 (COI), *Holler*, 29–8–1891 (NY); "Monte Rhön," *G. Geheeb*, 1870 (c. fr., NY), "Rhöngebirge," *G. Geheeb*, 1869 (NY), Geisa Wald, *G. Geheeb*, 1873 (c. fr., NY); Hübelkuppe bei Geisa, in Vorder-Rhön, *G. Geheeb*, 16–11–1868 (c. fr., NY). Hessen: Laubach, Vogelsberg, *Röth*, 9–8–1903 (herb. Bartram FH, NY), *Röth*, 10–6–1885 (ex herb. Uggla NY). **Poland.** Silesia: Gralen bei Göbersdorf (Kreis Waldenburg), *J. & H. Milde*, 8–1869 (c. fr., NY). **Norway.** Gaset i Asker, *Kiaer*, 7–6–1878 (ex herb. Uggla NY). Akershus: Asker distr., Skaugumsåsen, *Fridts*, 10–9–1886 (c. fr., BCB); Grossaetdal, Asker, pr. Christiania [Oslo], *Kaalaas*, 29–5–1883 (c. fr., NY). Telemark: Tinn Distr., Rollag, *Kiaer*, 4–8–1890 (BCB). **Slovakia.** "Slovakia orientalis: montes Cerhovské pohorie," *Vána*, 29–5–1973 (NY). **Sweden.** Västergötland, Billingen, *Möller*, 9–8–1914 (herb. Bartram FH); Mösseberg, *Lindberg 18.23/6*, 22–6–1880 (NY), *Flink*, 25–6–1880 (MA); Våmb Billingen, *Hülphers*, Jun 1916 (c. fr., NY). Småland: Ljungarum, Rosenlund, *Arnell*, 9–1891 (NY). **Switzerland.** "Mtns. of Rhone valley," *G. Geheeb* (c. fr., NY).

Anomodon rugelii is distinctive in the rusty brownish color of the plant, the feltlike primary branches (due to the abundance of rhizoids), the more slender branches with strongly incurved leaves when dry, the redness of the costa, and, above all, the conspicuous auricles at the leaf base. Apiculate leaves are not a reliable character, as there are many plants whose leaves are obtuse to rounded and lack an apiculum. According to Ireland (1971), *A. rugelii* has foliose pseudoparaphyllia, but, mostly, they are completely uniseriate, as Ireland's (1982) later figures show. Multiseriate pseudoparaphyllia are uncommon in this species.

Even though they are nomina nuda, the names *Anomodon apiculatus* B.S.G. and to some extent also *Leskea apiculata* Schimp. in Müll. Hal. have been extensively used in older literature for *A. rugelii*. The apiculate leaf apex is a distinctive, if inconsistent, feature, and one can understand why so many authors have been drawn into using these names.

Some authors, including Iwatsuki (1963), recognize the variety *ferrugineus* (Besch.) Z. Iwats. (also applied to specimens named *A. uematsui* Broth.; *A. ferrugineus* (Besch.) Noguchi), on the basis of a more reduced habit, more delicate leaves, smaller auricles, and the lamina with an even more pronounced rusty tint (which accounts for the epithet). Leaves in these specimens are less incurved than in the type. In my opinion, this variability does not deserve formal taxonomic recognition. Leaves in many specimens of *A. rugelii* are not apiculate but rounded. Specimens from NE China (province of Jilin) and Japan show very reduced and inconspicuous leaf auricles; auricles may even be absent in some of the leaves on either side of the leaf insertion. Some leaves are even found to be decurrent, and occasional large round papillae are found on the back of the costa; in *A. rugelii* the costa is usually smooth abaxially. Nonetheless, these specimens do have the highly raised papillose-mammillose cells on the basal leaf margin and also the auricles, the most characteristic feature of *A. rugelii* (although sometimes dramatically reduced). This material could very well belong to what Iwatsuki considers subsp. *ferrugineus* (=*A. uematsui*), although this taxon is supposed to be an endemic of Japan.

One of the syntypes of *A. ramulosus* Mitt. (Japan, Nantaizan, collected by Bisset) is *A. rugelii*. The description is rather vague; because the most distinctive features of *A. rugelii* are not mentioned (rusty color, incurved, apiculate leaves with auricles), I am inclined to think that Mitten considered the specimen to belong to *A minor*.

3. Anomodon minor (Hedw.) Fürnr., Flora 12 (Erg. 2): 49. 1829. *Neckera viticulosa* var. *minor* Hedw., Spec. Musc. 210. 1801. *Neckera minor* P.-Beauv., Prodr. 78. 1805. *Neckera flaccida* Brid., Sp. Musc. 2: 137. 1812.—TYPE: U.S.A. Pennsylvania, Lancaster, *Muhlenberg* (as *Neckera viticulosa* var. *minor*, G-Hedw.-Schwaegr.!, c. fr.).

Hypnum viticulosum var. *brachycarpum* Müll. Hal., Syn. 2: 473. 1851.—SYNTYPES: U.S.A. *Drummond, Musci Amer. 163*; *Sullivant, Musci Allegen. 74.*

Anomodon integerrimus Mitt., J. Linn. Soc. Bot., suppl. 1: 126. 1859. *Anomodon minor* subsp. *integerrimus* (Mitt.) Z. Iwats., J. Hattori Bot. Lab. 26: 41. 1963.—TYPE: NEPAL. *Wallich* (lectotype, here designated: NY-herb. Mitten!).

Anomodon planatus Mitt., J. Linn. Soc. Bot., suppl. 1: 126. 1859.—TYPE: INDIA. Himachal Pradesh, Simla, "7000, 8000," *Thomson 1126*, Oct 1849 (lectotype, here designated: NY-herb. Mitten !).

Anomodon ramulosus Mitt., Trans. Linn. Soc. London, ser. 2, 3: 187. 1891.—TYPE: CHINA. Chekiang, Ningpo, *Oldham* (lectotype, here designated: NY!).

Anomodon platyphyllus Kindb., Ottawa Naturalist 7: 19. 1893.—TYPE: CANADA. Can. Musc. 256; Macoun Cat. Pt. VI, 171.

Anomodon sinensis Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 3: 118. 1896.—TYPE: CHINA. Shaanxi, "China bor. or., Si-Ku-tzui-san," *Giraldi*, 1894 (isotype?: FH!).

Anomodon leptodontoides Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 4: 275. 1897.—TYPE: CHINA. Prov. Shen-si sept., Schan-kio, *Giraldi*, Aug 1895 (FI).

Anomodon minor var. *inaequalifolius* Bartr., Bryol. 50: 207. 1947.—TYPE: GUATEMALA. Huehuetenango, Río Ocheval, pr. S. Miguel Acatlán, 29–12–1945, *Sharp 4857* (isotypes: FH-Bartram! MICH!).

Plants of median size, forming loose mats, dull green when dry, bright green when moist. Main stems creeping, branches to 2.5 cm long, exceptionally to 6 cm, (0.6–) 1.0–1.7 mm thick when dry (leaves included), erect-ascending to arcuate, julaceous when dry, primary branches not or seldom branched; central strand of stems poorly or not differentiated, pseudoparaphyllia absent. Branch leaves broadly decurrent, imbricate, sometimes slightly crisped when dry, erect to spreading, complanate, not secund when moist, broadly oblong-lingulate, (1.0–) 1.5–2.3 (–3.0) mm long, abruptly narrowed from an ovate base with undulate margins, sometimes dentate to spinulose at the insertion because of very high papillae and sometimes infolded into a rounded apex, generally widened; costa moderately robust and prominent on the back, pellucid, ending at (0.04–) 0.08–0.15 (–0.20) mm from the apex, often bifid, not obscured by laminal cells near the apex; cells on the back of the costa elongate (40–68 µm), with seriate globulose papillae; basal hyaline cells extending just 1/3 of the basal leaf portion or less, mostly papillose; medial laminal cells hexagonal, 7–12 µm wide, densely papillose, with high and branched papillae. Inflorescences occurring on terminal branches, beyond the distalmost branching points; perichaetial leaves with apical cells papillose. Seta 4–16 mm. Capsule ovoid; urn 1.5–2.2 mm long, without stomata, annulus well developed; operculum obliquely short-rostrate, 0.35–0.6 mm; exostome reduced, irregular, up to 0.34 mm high, teeth papillose above, not striolate below, often trabeculate; endostome very reduced, consisting of a papillose basal membrane, no more than 2 cells high (ca. 0.035 mm) and segments ca. 0.045 mm high, irregular and fragmentary. Calyptra smooth. Spores (11–) 13–18 (–21) µm in diameter, almost smooth to faintly papillose. Chromosome number: n = 11 (in meiosis, North Carolina: Granzow-de la Cerda, 1988b).

Distribution (Figs. 19, 20). South and East Asia, from far eastern Russia, Manchuria, Korea, and Japan to Burma and the Himalayas; all of eastern North America to New Mexico, highlands of Mexico and Guatemala; absent in Europe. *Anomodon minor* occurs in deciduous forests, where it grows on calcareous rocks as well as on tree bark and forms loose, thin, somewhat discontinuous mats. In North America it requires the most mesic habitats and fruits infrequently.

Representative Specimens. **Bhutan.** Oongar, *Griffith* (as *A. integerrimus*, herb. Mitten NY). **China.** Heilongjian: Manchuria, Muling, *Sinzew* (NY). Chihli: I Yuan K'on, *Clemens 5098*, 28–4–1913 (NY). Hubei: Shennonjia Forest Distr., Jizigon, *Sino-Amer. Exp. 882*, 25–8–1980 (as *A. thraustus*, NY). Jiangsu: Nanjing, Oixia Mt., *Li Zihua 59*, 24–6–1963 (NY, MICH), "Kiang Su," *S. Henry*, 4–11–1907 (NY). Jilin: Chang Bai-shan, *Guo Qian 22235*, 23–9–1981 (as *A. integerrimus*, c. fr., NY); distr. Linjian, Hualazi shan, *Guo Qian 7764*, 8–9–1963 (as *A. planatus*, IFSBH); An tu, Erdo Bai xi zien, *Koponen 36559*, 20–9–1981 & *37252*, 25–9–1981 (as subsp. *integerrimus*, JE). Liaoning: distr. Feng Cheng, Tong Yuan Bao, *Guo Qian 6016 & Nan Man Ling*, 6–7–1961 (IFSBH). Xishuangbanna: Mengla Bot. Trop. Garden, *P. Redfearn et al. 33987*, 25–12–1986 (as *A. viticulosus*, NY). Yunnan: Pe yen tsin, *Sommer* 1921 (as *A. thraustus*, JE); Kweitschou, "ad viam Tschenning-Huang-tsanba," *Handel-Mazzetti 2037* (10.424), 23–6–1917 (JE). **India.** Nubra, *Thomson*, 27–3–1848 (NY). Himachal Pradesh: Simla, *Thomson 1105*, Oct 1849 (NY). Kumaon: Kapkate, *Walker 459*, Sep 1899 (as *A. planatus*, c. fr., herb. Bartram FH, MICH). Madras: Palni hills, Kodaikanal area, *P. Foureau 1268* (as *A. plicaefolius*, NY). Mussoorie: NW Himalaya, Dhanoulti, *Bahadru*, 10–12–1903 (as *A. integerrimus*, c. fr., Brioth. Levier NY); "Botanical Garden," *Gollan*, 7–8–1900 (as *A. glossophyllus*, c. fr., NY); "below Old Bot. Garden," *W. Gollan*, 26–11–1903 (as *A. planatus* JE). "India orientalis": *Bell 119, 120, 367* (ex herb. Mitten NY). **Japan.** Honshu: Aichi pref., Mt. Mikawa-Hongûsan, *Takaki 3898*, 11–9–1947 (NY); Bungo, "Kannawa," *Iwasaki 1740*, 10–9–1916 (as *A. thraustus*, NY); Higuo pref., Sübara-machi, Yatusiro-gun, *Tasiro 3340*, 16–1–1940 (NY); Mie pref., Mt. Fujiwara, *T. Hoguro 34*, 19–10–1965 (c. fr., as *A. subintegerrimus*, NICH); Kawakani, Misugi, *T. Nakajima*, 22–8–1963 (as subsp. *integerrimus*, exicc. Noguchi 952, JE, MICH, NY), Isejingu, (*N. Takaki 4467*, 28–3–1948 (as *A. integerrimus*, NICH); Mikawa, Miwamura, Chichiiwa, (*N. Takaki 11333, Y. Horikawa*, 26–3–1950 (as *A. integerrimus*, NICH), "South Alps," (*N. Takaki 11787*, 20–7–1952 (as *A. planatus*, NICH); Nikko, *Kamiji 85*, Aug/Sep 1947 (herb. Bartram FH); Okayama pref., Rashômo, Niimi, *Igi*, 15–1–1958 (as *A. integerrimus*, exicc.

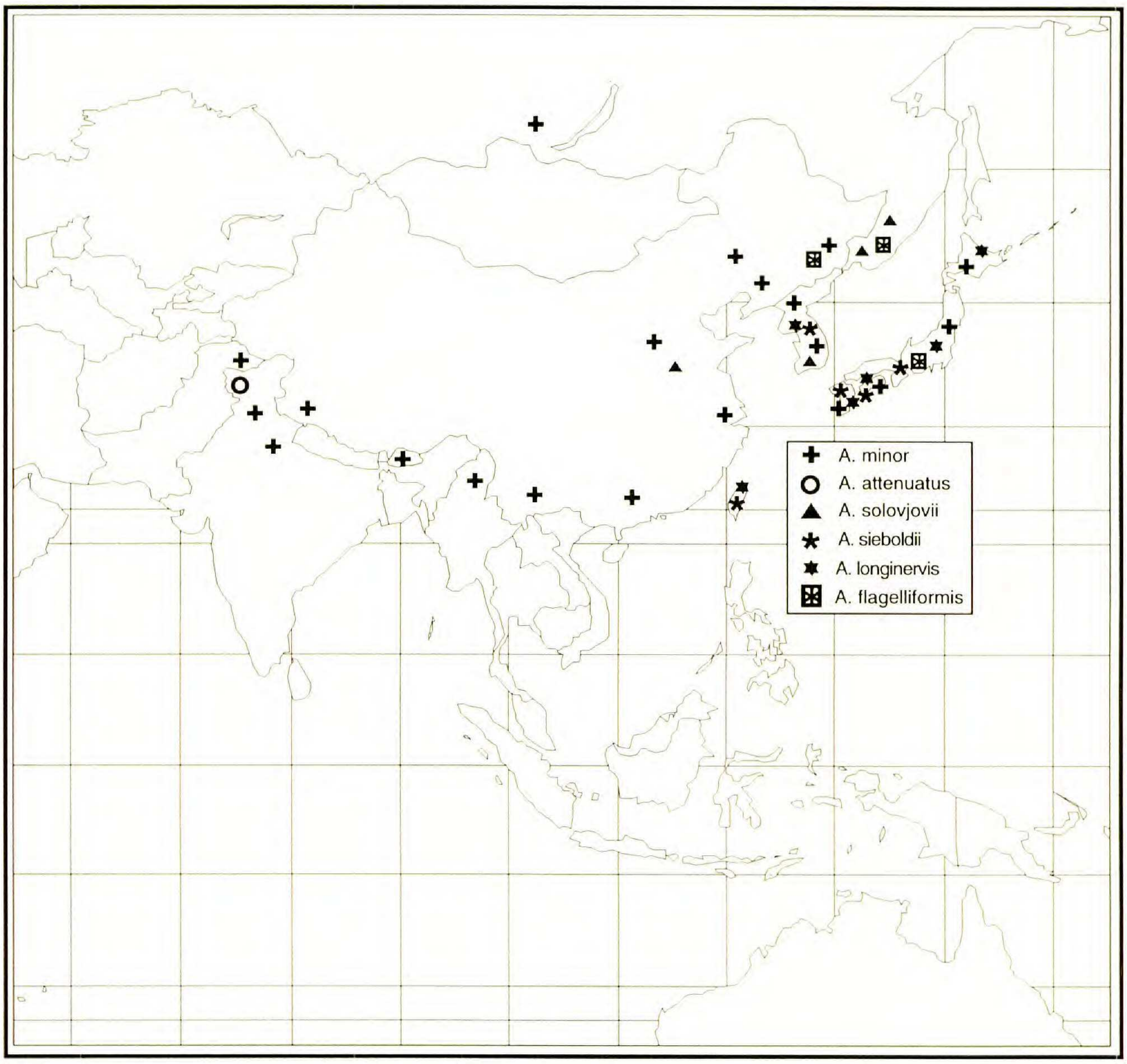


FIG. 20. Distribution of *Anomodon attenuatus, A. flagelliformis, A. longinervis, A. minor, A. sieboldii,* and *A. solovjovii* in central and eastern Asia.

Noguchi 654, NY); Osaka Pref., Takatsuki, Hara, *T. Nakajima*, 29–4–1960 (as *A. minor* subsp. *integerrimus*, HIRO, MICH, NY); Tokyo pref., Nishitama-gun, Nippara, *R. Watanabe 13928*, 8–8–1967 (as *A. ramulosus*, NICH). Kyushu: Fukuoka pref., Kawara-machi, *Kuwahara 2771*, 26–8–1952 (NY); Kumamoto pref., Hitoyoshi, *Mayebara*, Jan 1948 (as *A. ramulosus*, JE, MICH); Miyazaki pref., Nishimera-mura, *Z. Iwatsuki 4806*, 5–2–1980 (as subsp. *integerrimus*, NY); Yabakei, Buzan, *Iwasaki 534*, 29–8–1916 (NY). Shikoku: Kôchi, Toja, *S. Okamura*, 10–12–1905 (FI, herb. Bartram FH); Tosa, Tosayoma, *Gono 247b*, Jan 1904 (FI, herb. Bartram FH). **Korea.** *B. Sauer*, 1924 (JE); Fusan: *Faurie 72*, Oct 1901 (FI). Hysyeng Yang: *Faurie 80*, Jun 1901 (FI); Mt. Chiak, *W. Hong 5877, 5887*, 16/17–7–1961 (as *A. integerrimus*, NICH); Mt. Chii, *W. Hong 1978, 2082*, 16,17–8–1960 (as *A. integerrimus*, NICH); Mt. Sam-sung, *W. Hong 1508*, 3–4–1960 (as *A. integerrimus*, NICH); Mt. Sokri, *W. Hong 2816*, 21–12–60 (as *A. integerrimus*, NICH). **Russia.** "Regio Iskutkensis, distr. Czeremchovo, Mts. Sajanenses orientales," *L. Bardunov & S. Lipin*, 17–7–1959 (as *A. planatus*, NICH).

Canada. Manitoba: Red River, St. Norbert, *Bird 3269*, 28–5–1959 (c. fr., DUKE); Parkland, N of Glenboro, *C. Bird 5953*, 13–5–1961 (c. fr., FH, MICH); Winnipeg, SE of Hadashville, *Mueller-Dumbois*, 9–4–1961 (FH). Ontario: Edmonton, *White*, 10–11–1893 (as *A. platyphyllum*, c. fr., NY); Ottawa, *J. Macoun*, 3–10–1892 (as *A. obtusifolius*, DUKE, c. fr., FH); Thunder Bay, Sturgeon Bay, Blake Twp., *C. Garton 19834*, 5–5–1981 (MICH); "about Falls of Niagara," *Drummond* (MICH). Québec: Com. Montcalm, Park du Mont Tremblant, *F. Hermann 16612*, 19–7–1961 (MICH); Chelsea, *J. Macoun*, 17–5–1907 (MICH). **Mexico.** Chiapas: Las Casas, *A. Sharp 3515*, 26–4–1945 (DUKE, MEXU, MICH, NY). Chihuahua: Parque Nac. Cascada de Basageachi, *A. Whittmore 2857 et al.*, 4–10–1986 (MEXU).

Guerrero: Chilpancingo, 25 km W, *A. Sharp 1052*, 22–10–1944 (MEXU, MICH), ca. 22 km W, *A. Sharp 1096*, 27–10–1944 (MICH), Omiltemi, *A. Sharp 1132 & 1133b*, 27–10–1944 (MICH, & FH, MEXU, NY). Jalisco: La Cumbre, 10 mi SW of Autlán, *H. Crum 458a*, Jun 1949, *H. Crum 514a*, Aug 1949 (MICH). Morelos: Cerro Tepozteco, *C. Delgadillo*, 28–9–1991 (MEXU). Oaxaca: San Pablo Ayutla, 70 km E of Oaxaca, *A. Sharp 4609 et al.* (MEXU). **U.S.A.** Alabama: Jackson Co., Pint Rock, *I. G.-de la Cerda 1109 & E. Lyons*, 4–2–1984 (DUKE). Arkansas: Marion Co., Flippen, *L. Anderson 12317*, 12–6–1953 (DUKE); Stone Co., Ozark Mts., White River, *L. Anderson 11596*, 18–5–1953 (DUKE), Blanchard Springs, *D. Demaree 28855*, 30–4–1950 (DUKE). Illinois: Laramie River (c. fr., as *A. obtusifolius*, JE); Athens, *Hall & Hartman*, 1879 (c. fr., JE); Chicago, *Röll*, 1822 (as *A. obtusifolius*, FH). Indiana: Parke Co., Turkey Run St. Park, *W. Welch 11482*, 13–11–1937. Iowa: Pottawatamie Co., W of Crescent *S. Churchill 7109*, 18–6–1976 (c. fr., FH). Kansas: Salina, *Henry* (as *A. obtusifolius*, FH). Maine: Pea Cove, *E. Merrill 126*, Oct 1898 (FH); Spencer's Woods, *Anthony 2413*, 16–4–1888 (c. fr., DUKE); Oxford Co., Norway, *Bacon 8942*, 5–5–1929 (DUKE). Massachussetts: Amesbury, *Huntingdon* (JE); West Townsend, *Thomson*, 24–9–1935 (FH). Michigan: Miner's Castle, *W. Steere 594*, Jul 1933 (FH). Minnesota: Winona Bluffs, *J. Holzinger*, 2–12–1899 (c. fr., FI); Benton Co., *Henry*, 9–1885 (JE); Chippewa Co., pr. Montevideo, *J. Holzinger* 15–6–1901 (c. fr., FH). Missouri: Hannibal, Mark Twain's Cave, *Davis*, 7–11–1911 (FH); Cooper Co., S of Blackwater, *A. Sharp*, 7–10–1938 (FH); Franklyn Co., Merramec Rvr., *B. Allen 6109*, 30–1–1988 (MICH). New York: McLean Bog, Cornell Univ., *Kauffman*, 25–10–1902 (as *A. obtusifolius*, c. fr., FH). New Jersey: Closter, *Austin* (FH). North Carolina: Alleghany Co., Roaring Gap, *L. Anderson 1273*, 18–8–1933 (DUKE); Grandfather Mtn., *Small & Heller 20*, 25–7–1891 (c. fr., DUKE); Jones Co., Coastal Plain, Trent river, Trenton, *L. Anderson 10819*, 20–4–1952 (DUKE); Mitchell Co., Roan Mtn., *A. Weakley*, 1984 (DUKE); Orange Co., Eno River State Park, *I. G.-de la Cerda 1938*, 31–11–1984, (c. fr., DUKE), *I. G.-de la Cerda 1942, 1943*, 7–12–1984 (DUKE). Ohio: Columbus, *Schraeder* (c. fr., as *A. obtusifolius*, JE); ibid. *Sullivant*, 1850 (c. fr., JE). Pennsylvania: Huntingdon Co., Spruce Creek, *A. & P. Felton & I. G.-de la Cerda 1853*, 30–9–1984 (DUKE); McKean Co., *Burnett 2831*, 7–11–1897 (c. fr., FH). South Dakota: Day. Co. Wanbay Nat. Windlife Ref., *S. Churchill 7826*, 24–6–1976 (FH); Robert Co., Harford Beach St. Park, *S. Churchill 7807*, 23–6–76 (FH). Tennessee: Knox Co., Island Home, *A. Sharp 3532*, 3–3–1935 (FH). Texas: Culberson Co., Guadalupe Mtns., McKittrick Canyn, *Moore & Steyermark*, 2–7–1931 (FH). Vermont: Manchester, Lye Brook, *A. Grout*, 23–4–1892 (as *A. obtusifolius*, c. fr., DUKE); Newfane, *A. Grout 2416*, 25–7–1902 (DUKE). Virginia: Marion, *A. Vail & E. Britton*, 6–6–1892 (as *A. viticulosus*, MICH); Giles Co., Mountan Lake, *Blomquist 3261*, 3–8–1934 (FH); Smyth Co., Whiteface Mountain, *M. Bucher & A. Weakley*, Oct 1984 (DUKE). West Virginia: Pendleton Co., South Branch of Potomac, *Boardman*, 29–5–1938 (DUKE). Wisconsin: Richland Co., Hub City, *Hermann 28308*, 21–5–1978 (DUKE).

Some slender specimens of *A. minor* with branch leaves that are not complanate when moist and a costa that becomes obscured by dorsal laminal cells near its end (the latter is the case of Hedwig's type material from Pennsylvania) resemble those of *A. thraustus*. In *A. minor* the upper part of the costa remains pellucid for most of its length and often becomes bifid before ending, whereas in *A. thraustus* the costa is obscured by dorsal laminal cells for the upper 1/3 of the leaf or more. Occasionally, in such specimens the upper portion of the leaves may also be broken off, as in *A. thraustus*. The delicate, narrowly lingulate upper leaf portion of *A. thraustus* is still distinct, whereas that of *A. minor* is wider and proportionally shorter. Larger specimens of *A. minor* with non-complanate leaves can be told apart from *A. viticulosus* by their more slender habit and smaller leaves, imbricate when dry and not secund when moist. *Anomodon viticulosus* also has more congested, secund branch leaves.

Certain specimens, mostly from East Asia, seem intermediate between *A. minor* and *A. rugelii*. Often specimens of *A. minor* have strongly spinulose basal marginal cells, like those of the auricles of *A. rugelii*. The lack of auricles and the thick papillae on the back of the costa remain good characters for separating both species, although it is also true that the presence of obvious papillae on the back of the costa in *A. minor* is not absolutely consistent. Characters that traditionally have been taken as of great taxonomic value for both *A. minor* and *A. rugelii* may be found mixed, and therefore such value is questionable. Apparently, the only characters that remain congruent with each other are the auricles (sometimes extremely reduced) and foliose pseudoparaphyllia of *A. rugelii*; both structures absent in all specimens of *A. minor*. Therefore, these two characters always keep both species distinct, in spite of the presence of superficially intermediate forms that seem to indicate a blending of these two taxa.

Iwatsuki (1963) recognized *A. minor* subsp. *integerrimus* (Mitt.) Z. Iwats., as the taxon occurring in Asia and restricted subsp. *minor* to eastern North America and Central America. According to Iwatsuki, subsp. *integerrimus* differs from the subsp. *minor* in having very slightly larger spores, some irregularity in the pinnate branching pattern of primary branches, as well as asymmetric branch leaves caused by a narrowing of the lamina toward the leaf base, therefore becoming slightly falcate-secund. In practice, however, the distinctions barely stand in this rather variable species. I have chosen to recognize only a single taxon, *A. minor*.

The name *A. planatus* Mitt. has been used for some smaller forms of *A. minor* with leaves up to 1.2 mm long. Of all segregates of *A. minor* this is probably the most clear-cut and its recognition understandable. The name has been used, however, mostly for specimens of *A. minor* collected in the southern Himalayas, for no apparent morphological reason. Iwatsuki (1963) included *A. planatus* Mitt. in his *A. minor* subsp. *integerrimus*. However, mixed in Mitten's type material (NY!) are specimens that correspond to *A. thraustus* (for lectotypification of *A. integerrimus* and *A. planatus*, see the discussion for *A. thraustus* below). Another taxon, *A. minor* var. *inaequalifolius* Bartr. (Bartram 1947, 1949), from Guatemala (Huehuetenango: Río Ocheval, near S. Miguel Acatlán, *A. Sharp 4857*, 29–12–1945, type, herb. Bartram in FH!), is almost identical with Iwatsuki's subspecies. I consider all these variations within the confines of *A. minor*. *Anomodon ramulosus* Mitt. is a robust form that somewhat resembles *A. rugelii* in habit because of its narrower and longer leaves (leaves are slightly incurved, or "curly"). Only the syntype from China, Ningpo, collected by Olden is *A. minor* (one of the others is actually *A. rugelii*). Because the only discriminating character provided in the protologue is "foliage on some stems is subcompressed," I consider it appropriate to designate the Ningpo specimen of *A. minor* (Oldham's collection, NY!) as the lectotype for *A. ramulosus*.

The name *Anomodon obtusifolius* Bruch & Schimp., has been extensively used until the turn of this century, mostly for North American specimens of *A. minor*; however, because Bruch and Schimper (1848) based it on Hedwig's *Neckera viticulosa* var. *minor*, which had already been elevated to specific status 19 years earlier, it is a superfluous name. *Anomodon obtusifolius* Bruch & Schimp. is not to be confused with *A. obtusifolius* Mitt. (a nomen nudum), which has been applied to some East Asian specimens of *A. viticulosus*.

I.a.ii. Anomodon subsection **Abbreviati** (Z. Iwats.) Granzow, comb. nov. *Anomodon* sect. *Abbreviati* Z. Iwats., J. Hattori Bot. Lab. 26: 51. 1963.

Branch leaves broadly oblong-lingulate, constricted near the middle into a wide upper portion, apex entire; costa not obscured in its distal portion by laminal cells; laminal cells with high mammillae, acute, spiny, generally single, or at least with one large central mammilla, with 1–3 smaller, unbranched papillae at its base. Capsules immersed or exserted on a seta 2–3 mm long.

4. Anomodon abbreviatus Mitt., Trans. Linn. Soc. Bot., ser. 2, 3: 187. 1891.—TYPE: JAPAN. Joshim, *Bisset*, Apr. 1886 (holotype: NY!). Fig. 21.
Anomodon asperifolius Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 3: 117. 1896.—TYPE: CHINA. Shaanxi, "Shen-si septentr., reg. montanae," *Giraldi*, 1894 (isotypes: FI-herb. Biondi! G!).

Plants robust, dark green, branching pattern simple, consisting of a creeping stem with primary branches 4–5 (–8) cm long, occasionally secondarily branched. Central strand of the stem not differentiated. Branch leaves erect-spreading, secund when moist, 2.8–3.5 (–4.8) mm long, abruptly narrowed at the middle; leaf base oval-lanceolate, upper 1/2 to 2/3 tapering to an acute, occasionally obtuse apex; costa strong and prominent at the back, with elongate cells, ca. 30 μm long, 23 μm or less in the distal portion, flexuose toward the apex, ending a few cells below, neither bifid nor obscured by laminal cells at the end. Lower cells hyaline, well differentiated, extending 1/4 up the basal portion of lamina; laminal cells 13–18 μm, incrassate and with round lumen in cross section, with a single, unbranched, tall, sharply conic central papilla on either surface, somewhat arcuate and pointing toward the leaf apex, as high or higher than the cell's lumen in cross section, with 2–3 short, sharply conic, basal papillae. Perichaetial buds on terminal branches; perichaetial leaves, somewhat longer, more lingulate, and with more elongate cells than the branch leaves, with papillose cells. Seta (1–) 2–3 mm; urn (1.1–) 1.3–1.8 mm long, ovoid to ovoid-elliptic, annulus present, stomata absent; exostome teeth ca. 0.27 mm long, sometimes trabeculate, verrucose above, smooth at the base or very slightly striolate; endostome absent or reduced to a few thin segments without a basal membrane. Spores 14–24 μm in diameter. Chromosome number unknown.

Distribution (Fig. 22). Japan (in the four larger islands), central and northeastern China, and Korea.

REPRESENTATIVE SPECIMENS. **China.** Liaoning: Kuandian, Bai shi laji Mtns, *W. Buck 23778*, 21–8–1993 (NY). Shaanxi: *Ibaraki*, 25–5–1900 (as *A. ramulosus*, ex herb. Paris FI). **Japan.** *Ibaraki*, 25–5–1900 (as *A. ramulosus*, ex herb. Paris FI); Bungo, Mt. Tsurumi, *N. Iwasaki 1229*, 25–9–1921 (NY); Awa, Mt. Tsurugi, *M. Kamimura 2621*, Aug 1936 (NICH); Higo, Gokanoso, *H. Kaneda 212*, 30–7–1935 (NICH); Kii, Odaigahara, *N. Takaki 4885*, 3–8–1948 (NICH); Musashi, Mt. Mitsumine, *N. Takaki 4535*, 9–4–1948 (NICH). Hokkaido: Iburi, nr lake Shikotan, *N. Iwasaki*, 18–10–1914 (NICH). Honshu: Fukushima pref., Tamura-gun, Mt. Ootakine, *T. Higuchi 1564*, 13–6–1953 (NICH); Hiroshima pref., Mt. Kammuri, *S. Nakanishi*, 8–11–1960 (JE); Hyogo pref., Mt. Sappico, N of Hmaji, *T. Kodama* 5–4–1962 (c. fr., NICH); Kinkwasan, *A. Noguchi*, 8–6–1929 (herb. Bartram FH); Kanagawa pref., Hakone Mts., *Redfearn 768-J-54*, 16–5–1954 (DUKE); Kotuke (?), Mt. Okeci, *A. Esumoda (?)*, 15–11–1912 (Herb. Bartram FH); Mie pref., Iishi-gun, Misugi-mura, Kawakami, *Nakajima*, 4–3–1963 (c. fr., JE), *Z. Iwatsuki 93*, 2/5–12–1963 (NICH); Miyagi pref., isl. Kiuzakan, *T. Higuchi 1195* 4–3–1953 (NICH), Oshika-gun, Mt. Kinka, *T. Higuchi 1195*, 4–5–1953 (NICH); Musasaki, Titibu-me, *M. Yano 5193*, 24–5–1920 (Herb. Sasaoka NY); Nagano pref., Iida, Matsu river, *M. Higuchi* 9–8–1980 (NICH), Kamiina-gun, Mt. Senjogadake, *R. Watanabe 18808*, 24–7–1973 (NICH), Kisofuku-shima, *Schofield 52003*, 17–10–1972 (DUKE), *Takaki 6402*, 27–6–1949 (NY), Minami Zumi-gun, Azumi-mura, *R. Watanabe 11425*, 13–8–1964 (NICH), Shimoina-gun, Mt. Toyokuchi, *R. Watanabe 9389*, 9–8–1963 (NICH); Niigata pref., Mt. Yahiko, *Y. Ikewani*, Mar 1948 (JE); Saitama pref., "Japonia centralis," Chichibu, *H. Mayr*, 9–5–1890 (ex herb. Broth. FH, FI, NY), Mt. Mitsumina, *N. Takaki 4535*, 9–4–1948 (NY), Chichibu-gun, Icirikanon, *R. Watanabe 14400*, 20–8–1968, (c. fr., NICH); Shimano, "Mt. Yatsu," *E. Iishiba*, 26–7–1908 (DUKE); Shizuoka pref., Honkawane-cho, Kanzoo, *Z. Iwatsuki*, 15–9–1959 (NICH); Wakayama pref., Mt. Gomadan, *M. Micutani*, 12–9–1949 (DUKE, NY); Yamanashi pref., Ashiyasu, *S. Inoue*, 20–8–1974 (JE), Mt. Kita-dake, *R. Watanabe 16701*, 12–8–1972 (NICH). Kyushu: Kumamoto pref., Mt. Kurobaru, *K. Mayebara 131*, May 1984 (JE, MICH, NY); Gokagoe (Mumimi), *Y. Kuwahara 2163*, 13–8–1951 (NY); Miyazaki pref., Koyu-gun, *Z. Iwatsuki 2316*, 6–5–1976 (NY), Nishiusuku-gun,

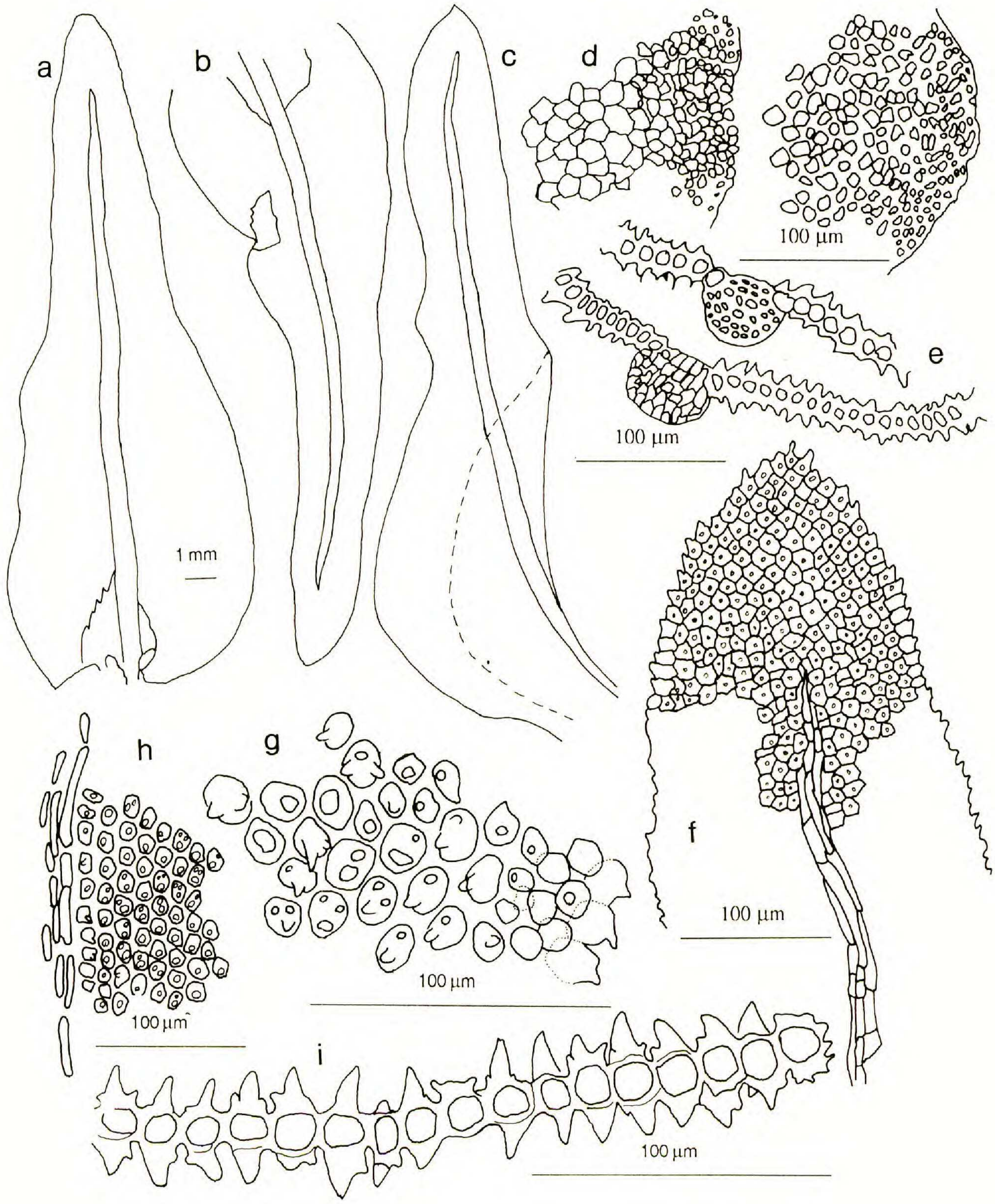


FIG. 21. *Anomodon abbreviatus* Mitt. a–c, branch leaves; d, cross section of stems without differenciated central strand; e, cross sections of branch leaves; f, apex of a branch leaf; g, h, leaf cells; i, leaf in cross section. Based on: a, d, Japan (loc. ignot., DUKE); b, e, f, *E. Iishiba*, Japan, Shimano, Mt. Yatsu, 26–7–1908 (DUKE); c, i, *Yano, 5193*, Hondo, "prov. Musasi, Titibu-me," 24–5–1920 (NY); g, h, *Schofield 52033*, Nagano pref., Kisofuku-shima, 17–10–1972 (DUKE).

Mt. Shiroiwa, *N. Suzuki & M. Kakuchi 12* (c. fr., NICH). Shikoku: Ehime pref., Kamiukena-gun, Omogo-kei, *R. Watanabe 20205*, 25–8–1973 (NICH); Tosa, Mt. Yokogura, *M. Kamimura 5100*, 24–7–1937 (NICH). **Korea.** Mt. Chii, 1250 m, *W. Hong 1225*, 16/23–8–1959 (NICH).

The habit and leaf outline of *A. abbreviatus* resemble that of *A. viticulosus*, but the characteristic large sharp central papilla on leaf cells of *A. abbreviatus* prevents confusion. *Anomodon solovjovii* could be mistaken for *A. abbreviatus*, but the latter is more robust, and the papillae are higher (more than the laminal

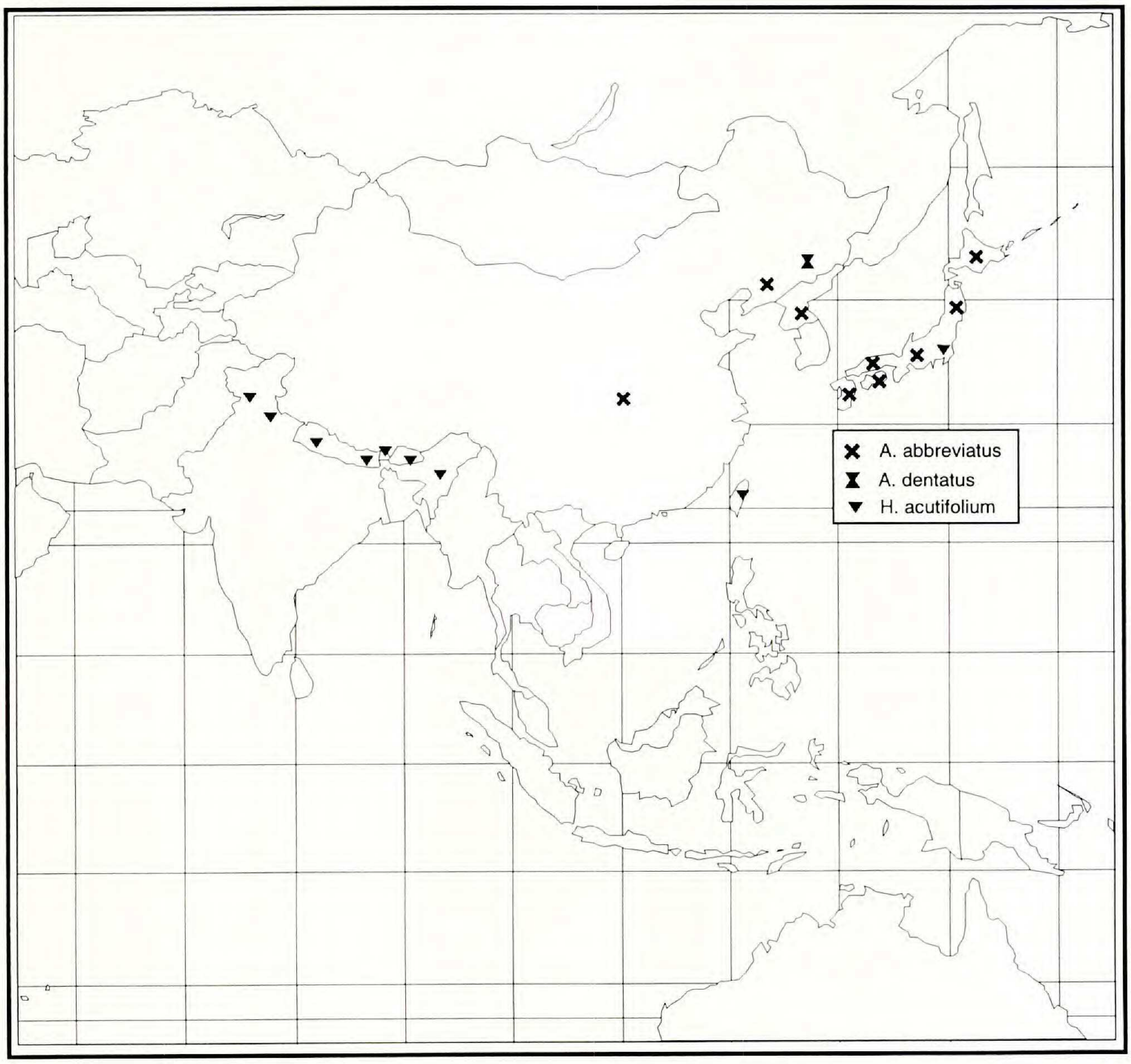


FIG. 22. Distribution of *Anomodon abbreviatus*, *A. dentatus*, and *Herpetineuron acutifolium* in central and eastern Asia.

cell's diameter in cross section). Setae are short in *A. abbreviatus*, but the capsules are exserted, whereas in *A. solovjovii* they are immersed, partly owing to the long perichaetial leaves of *A. solovjovii*.

5. Anomodon solovjovii Lazarenko, Rev. Bryol. Lichénol., 5: 45. 1933.—SYNTYPES (n.v.): RUSSIA. "Südussurisches Gebiet, Murawjow-Amurkij's Halbinsel, Umgegenden der Stadt Wladiwostok": "Eisenbahnstation Sedanska," *Solovjov*, 28–8–1930, "Eisenbahnstation Okeanskaja," *Solovjov*, 19–8–1930; Schamara-Bucht, Schkotowo- Bezirk, Maj-che rivers, *Solovjov*, 26–8–1930; "Im Walde an dem Korjawaja-Fluss," *Solovjov*, 7–9–1930. [All collected on stems of *Acer mono* and *Carpinus cordatus*.]

Anomodon solovjovii var. *henaensis* Tan, Boufford & Ying, Acta Bot. Yunnanica 18: 69, 1996.—TYPE: CHINA. Henan Prov., Neixian Xian: N of Xiaguan, *Boufford et al. 26458-B*, 4–6–1994 (holotype: FH!).

Plants moderately robust; primary branches 3–6 mm long, 1.0–1.2 mm thick when dry, scarcely branched; secondary branches erect. Central strand not differentiated. Branch leaves erect when dry, 1.4–2.0 mm long, secund when moist, crowded and spreading at branch apices, broadly oblong-lingulate, abruptly narrowed at the middle from a broadly ovate base into an obtuse, more often rounded apex; hyaline cells at the base reaching less than 1/4 the height of the portion of the lamina below the shoulders. Costa strong, ending near the apex (less than 200 μm), upper portion becoming diffuse, obscured by short laminal cells on the dorsal surface. Laminal cells with a single papilla on both surfaces; papillae arcuate, pointing toward the apex, their height less than the cell lumen in cross section, never branched but sometimes with 2–3 smaller papillae at the base. Inflorescences on terminal branches. Perichaetial leaves much longer than branch leaves, also more lingulate and the cells more elongate, with papillose cells. Seta usually less than 1 mm long. Capsules immersed, obovate, urn ca. 0.8 mm long, annulus well differentiated; peristome teeth papillose above, almost smooth below; segments of inner peristome rudimentary on very low basal membrane, finely papillose; spores 16–30 μm in diameter, minutely papillose; calyptra cucullate with globulose papillae in the upper half. [Sporophytes not seen; description taken from the protologue (Lazarenko 1933) and from Iwatsuki (1963)]. Chromosome number unknown.

Distribution (Fig. 20). The Russian Far East (south of the Ussuri river, region of Javarovsk), Henan province in China, and Korea. *Anomodon solovjovi* grows on tree trunks at medium elevations.

ADDITIONAL SPECIMENS EXAMINED. **Korea.** Mt. Odai, *W. Hong 2563, 2621*, 24 Oct. 1960 (only male plants, NICH). **Russia.** "Asia Borealis Orientale: reg. austro ussuriensis, fl. Ssputinka," *A. Lazarenko*, Oct 1934 (*ex* Verdoorn–255, JE, MICH, NY).

The outline and size of leaves are like those of *A. minor*, although the two species cannot be mistaken, given the tall, arcuate central papilla of leaf cells found in *A. solovjovii*. The areolation and papillae morphologies of *A. solovjovii* closely resemble those of *A. abbreviatus*. *Anomodon solovjovii* differs from this species by its smaller leaves, smaller laminal cells (14.3 μm at the most), and by having the end of the costa covered with dorsal lamina cells. Thus, the costa becomes papillose on the back; it does not appear as clearly defined as in *A. abbreviatus* and ends farther from the apex (more than 200 μm).

A disjunct population from the interior of eastern China was recently described as *A. solovjovii* var. *henanensis* (Tan et al. 1996). The variety, which was distinguished by the smaller size of the single papilla of the leaf cells, seems to be well within the variability of an otherwise poorly collected species, and in my opinion lacks sufficient merit to be segregated at the varietal level.

The species is named after the assistant at the Forestry Department at a Russian Far East University, K. P. Solovjov, whom made the first collections.

I.a.iii. Anomodon subsection **Dentati** Granzow, subsect. nov.—TYPE: *Anomodon dentatus* C. H. Gao.

Folia ramealia aliquantum grandia, oblongo-lingulata, nonnihil spatulata; apex margine valde serrato, plerumque effractus; costa prope apicem evanescens, subter laminae cellulis occulta.

Branch leaves narrowly oblong-lingulate to spatulate, abruptly constricted near the middle into a very narrow upper portion; apex strongly and irregularly serrate, often broken off; costa fading well below the apex, obscured by laminal cells; laminal cells with multiple branching papillae.

6. Anomodon dentatus C. H. Gao, Flora Muscin. China Boreali Orientale, 380. 1977.—TYPE: CHINA. Kirin, Tchangbaishan, "in truncis arborum silvaticarum," *Gao 1231*, 28–6–1958 (holotype: IFP!). Fig. 23.

Plants rather robust; branches pinnate, erect to arcuate, ascending. Leaves julaceous and somewhat flexuose when dry, secund or widely spreading to reflexed when moist, 2.2–4.0 mm long, narrowly oblong-lingulate, somewhat spatulate, abruptly constricted near the middle, base ovate, apex strongly and irregularly serrate, bistratose, often broken; margins flat. Costa reaching just short of the apex, obscured by laminal cells just above the constriction, becoming hardly visible toward the apex. Basal hyaline cells well differentiated, smooth, elongate, with more or less sinuose walls, forming an extensive group that occupies half the leaf base, gradually becoming shorter and rhomboidal and merging with the upper cells; median laminal cells pluripapillose, the papillae weakly branched. Perichaetia present on the most terminal branches, perichaetial leaves with cells papillose. Sporophytes unknown. Chromosome number unknown.

Distribution (Fig. 22). Endemic to the northeastern region of the China, known only from the provinces of Kirin (or Jilin) and Liaoning, in the mountain range of Tchangbaishan, somewhat close to the border with North Korea. According to the label of the type collection, this species grows on tree trunks.

ADDITIONAL SPECIMEN EXAMINED. CHINA. "Kirin [Jilin]: Tchangbaishan," *G. Qian 22108*, 24–9–1981 (as *A. attenuatus*, NY).

Anomodon dentatus is a distinctive species, which clearly differs from any other species of *Anomodon*. Although more delicate, it resembles *A. abbreviatus* and *A. viticulosus* in its leaf shape (lamina abruptly constricted, with a wide, ovoid basal portion and a long, narrow upper part). Its leaves, reflexed when dry, and the loss of the leaf apices remind of *A. thraustus*, although it is unlikely to be mistaken for any of these species or any other in the genus. The most characteristic features of *A. dentatus* are the pinnate branching pattern (more similar to species of section *Haplohymenium*) and shape of the leaves: linear above the constriction, wider and strongly serrate at the apex.

Anomodon dentatus was known only from the holotype (!) and the paratype (not seen; from province of Liaoning: "Chean-Schan, ad arborum radices," 1958). Upon examination of the type as well as another specimen (originally misidentified as *A. attenuatus*) from the same mountain range as the holotype, I conclude that *A. dentatus* is a well-defined species.

I.b. Anomodon section **Haplohymenium** (Dozy & Molk.) Granzow, comb. nov. *Haplohymenium* Dozy & Molk., Musci Frond. Ined. Archip. Indici, 127. 1946.—TYPE: *Anomodon sieboldii* (Dozy & Molk.) Granzow.

Plants well-differentiated by the slender, very delicate habit. Secondary branches often flagelliform. Branch leaves spreading when moist, <1.2 mm long, apex not broken off (except in *A. tristis*), obtuse to acuminate; costa ending well below the apex, 35–70% the length of the leaf, in some species obscured above the shoulders by laminal cells. Sporophytes small, urn ≤ 1.0 mm long. Calyptra hirsute.

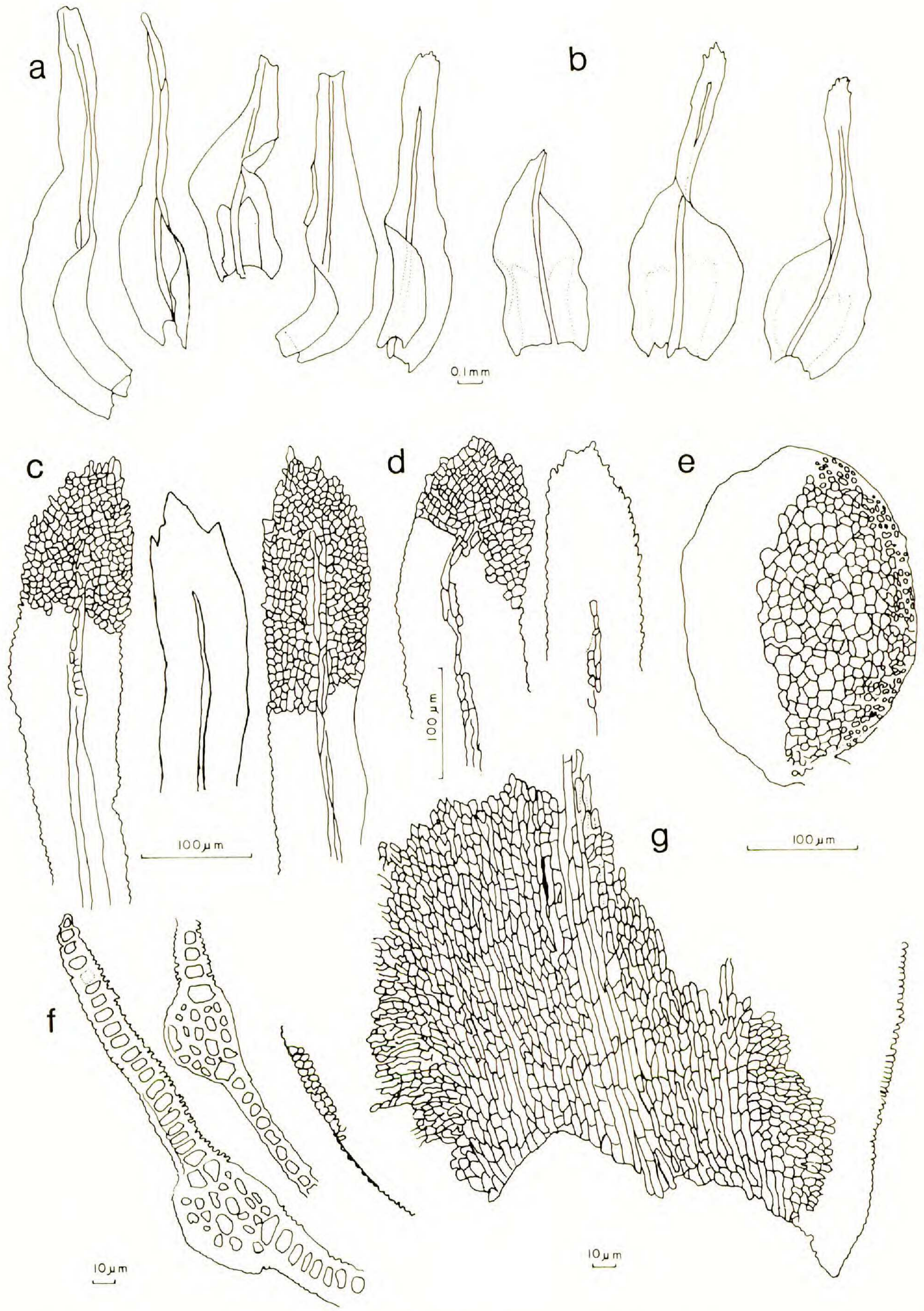


FIG. 23. *Anomodon dentatus* C. H. Gao. a, b, branch leaves; c, d, apex of branch leaves; e, cross section of branch; f, branch leaves in cross section; g, basal cells of branch leaf. Based on: a, c, e–g, *Guo Quian 22108* (NY); b, d, *Chen Gao 1231* (type), China, province of Kirin, Chang Bai-shan, (IFSBH).

7. Anomodon tristis (Ces.) Sull. & Lesq., Musci Bor. Amer. 52, 1856. *Leskea tristis* Ces. De Not., Syll. Musc. 67. 1838. *Hypnum triste* (Ces.) Müll. Hal., Syn. 2: 478. 1851. *Haplohymenium triste* (Ces.) Kindb., Rev. Bryol. 26: 25. 1899.—TYPE: ITALY. Lago Maggiore, Monte di S. Crescenzio, Verbanum, 1837, *C. Cesati* (holotype: RO!).

Anomodon fragilis Wilson, London J. Bot. 7: 275. 1848. *Hypnum fragile* (Wilson) Müll. Hal., Syn. 2: 471. 1851.—TYPE: CHINA. Chusan (n.v.).

Anomodon sinensi-tristis Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 3: 118. 1896.—TYPE: unknown.

Anomodon microphyllus Broth. & Paris, Rev. Bryol. 31: 56. 1904. *Haplohymenium microphyllum* (Broth. & Paris) Broth., Nat. Pflanzenfam. 1(3): 986. 1907.—SYNTYPES: JAPAN. Tsuruga, 14 Aug 1902, *Dampax & F. Gaultier* (n.v.); Tsu-Shima, May 1901, *Faurie 1662* (n.v.).

Anomodon fragillimus Herzog, Beih. Bot. Certralbl., 26: 82. 1909.—TYPE: BOLIVIA. Santa Cruz, Cerro Amboró, *Herzog* (holotype: JE!; isotypes: NY! US!).

Haplohymenium scabrum Broth., Rev. Bryol. Lichénol. 2: 10. 1929.—TYPE: RUSSIA. Siberia, prov. Primorskaja, Nikoljsk-Ussurijsk, pr. fl. Panicheza, *Ssemin* (n.v.).

Haplohymenium formosanum Nog., Trans. Nat. Hist. Soc. Taiwan 26: 43. 1936.—TYPE: TAIWAN. Tainan, Mt. Kodama, Aug 1932, *Noguchi 5867* (n.v.).

Haplohymenium fragiliforme Nog., J. Jap. Bot. 13: 410, f. 2. 1937.—TYPE: JAPAN. Sikoku, Mt. Yokogura, prov. Tosa, Aug. 1934, *Kamimura 648* (holotype: HIRO)

Haplohymenium longiglossum P. C. Chen, Feddes Repert. Spec. Nov. Regni Veg. 58: 31. 1955.—TYPE: CHINA. Prov. Szetschwan, Omei schan, Da-ping, 20–8–1842, *Chen 5353* (n.v.).

Plants very delicate and slender, filiform to wiry in appearence, forming lax mats, dull dark brownish green. Branches 0.5–1.5 cm long, 0.3–0.5 mm thick when dry; branching pattern simple, main stem creeping, sparsely branched into prostrate primary branches, which rarely branch themselves; central strand not differentiated. Leaves julaceous when dry, spreading, not complanate when moist, very delicate, 0.5–0.9 mm long, with apex (more often ca. 1/3 of the leaf) broken off, quite polymorphic among individual plants, lamina narrowing near the middle and tapering to an acute to acuminate or obtuse apex; margin flat, not papillose at the insertion, crenulate toward the apex because of very prominent papillae; costa short and delicate, pellucid below, ending below the middle of the leaf, obscured by laminal cells; basal laminal cells elongate, median ones round, ca. 4 µm, with multiple prominent papillae, thin-walled, cells of margins becoming mammillose toward the apex. Perichaetia rare, on terminal branches, perichaetial leaves oblong, acuminate. [Sporophytes not seen, but very similar to those of *A. sieboldii*, according to Noguchi (1957)]. Chromosome number: n = 11 (n = 9+H+h, in mitosis, Japan: Inoue, 1965).

Distribution (Fig. 24). *Anomodon tristis* is quite rare in Europe, where it is restricted to the eastern Alps, but rather common in eastern North America, west to the Ozarks and eastern Texas, with disjunct localities in eastern Arizona. It is present in Mexico, and reaches the highlands of South America (Bolivia, as *Anomodon fragillimus*). It also occurs in eastern Asia (eastern China, Japan, Taiwan) and Hawaii. No sporophytes are reported from Europe or the New World and are

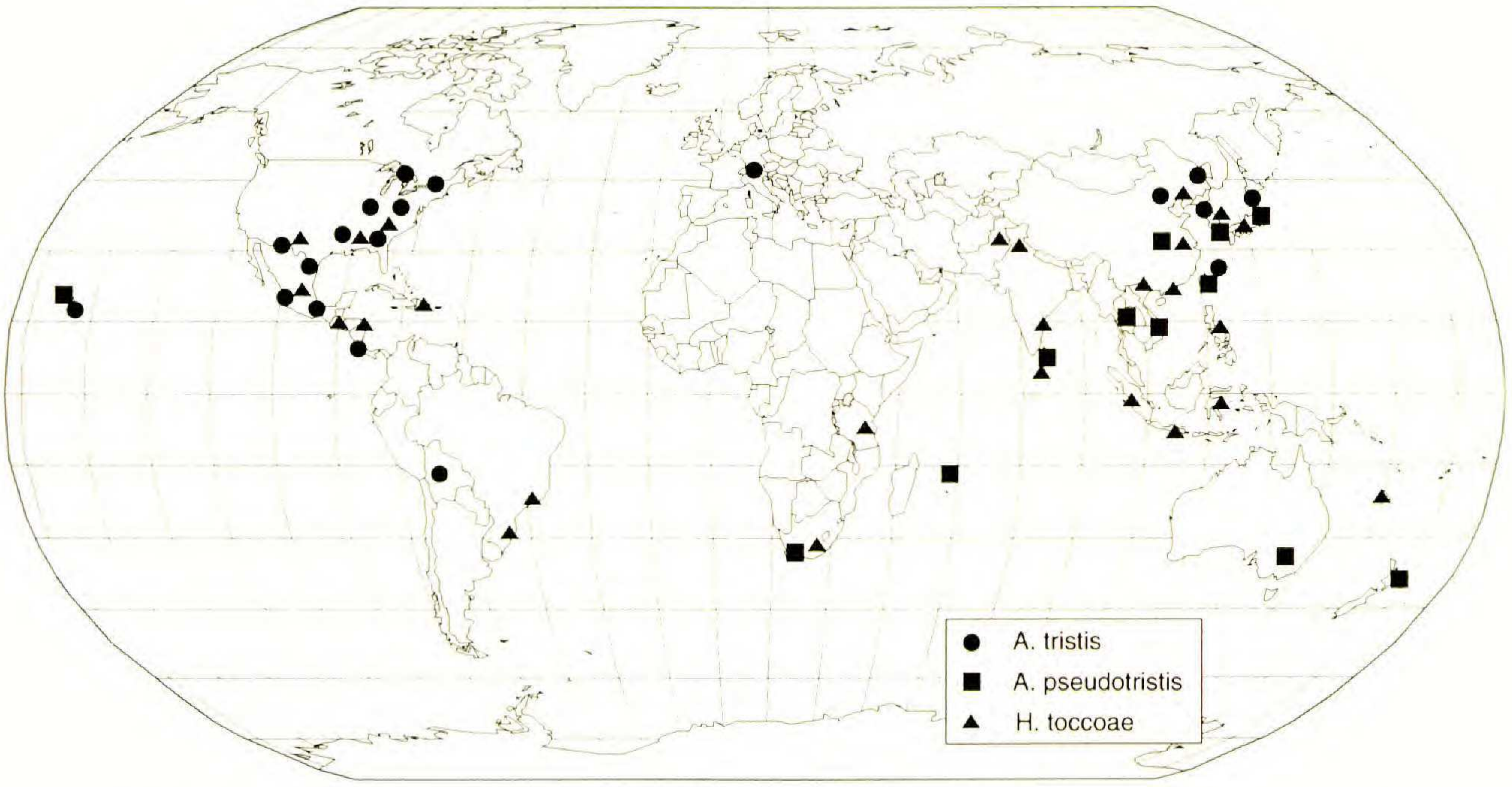


Fig 24. Distribution of *Anomodon tristis*, *A. pseudotristis*, and *Herpetineuron toccoae*.

rare in Asia. *Anomodon tristis* grows on bark of trees in deciduous forests in rather montane regions (except in eastern North America).

Representative Specimens. **China.** Hubei: Shenongjia Forest Distr. Quiujiaping to Mt. Laojun, *Sino-Amer Exped. 663A* (as *H. formosanum*, NY). Jilin: An-tu, NW Mt. Chang bai, *T. Koponen 37191*, 24–9–1981 (NY). Szechuan: Pe pei, pr. Chun king, mt. Tsin yun Shan, *P. C. Chen*, May 1940 (JE). **Japan.** "Japonia meridionalis," Omura (Hijeu), *J. Ferrié*, 15–1–1898 (FI). Honshu: Hiroshima pref., Tojô-shi, Hiva gun, *W. Schofield 54588 & T. Seki*, 18–4–1973 (DUKE), Miyajima Isl., Hiroshima Bay, *P. & A. Redfearn 33632*, 18–6–1985 (as *H. pseudotriste*, DUKE); Kanagawa pref., Hakone Mtns. Nat. Park, *P. Redfearn 720-J-54*, 16–5–1954 (DUKE); Miyagi pref., Sendai, *Y. Iishiba*, Nov. 1906 (JE); Osaka pref., Takasuki, Izuriha, *T. Nakajima*, 29–4–1960 (JE, MICH); Yamanashi pref., Kôfu-shi, Maizuru park, *T. Osada*, 6–4–1978 (MICH). Kyushu: Fukuoka pref., Mt. Hikasan, *Y. Kuwahara 2594*, 30–7–1952 (NY); Miyazaki pref., Minaminaka, Obi, *S. Hattori & T. Kurata*, May 1947 (JE, MICH). Shikoku: Kôchi pref. (prov. Tosa), *T. Makino*, 1887 (JE), Mt. Honokawa, *S. Okamura*, 31–12–1907 (FI). **Taiwan.** Taitu Hsien, Yehyu Tsun, *S. Lin* 169, 22–8–1975 (as *A. pseudotristis*, MICH). Taipei: Wulai Hsiang, betw. Fushan Tsun and Pling, *S. Lin*, 21/24–7–1973 (as *H. formosanum*, MICH); Tsang Po, Son Tcheou, *Courtois*, Feb 1908 (JE).

Hawaii. Maui: Haleakala Nat. Park, E of Kaupo Trail, below Paliku Pasture, *W. Hoe 4474*, 5–6–1977 (MICH).

Costa Rica. Heredia: S slope of Volcán Barva, 1 km WNW Río Ciruelas, 8.2 km from S. José de la Montaña, *M. Crosby 9894, 9923*, 3–5–1975 (MO). **Mexico.** Jalisco: Laderas de la Ferrería, Manantlán, *H. Crum 914A*, 23–7–1949 (as *A. minor*, NY). Nuevo León: Cerro de la Silla, pr. Monterrey, *L. Harvey 1022b*, 23–6–1939 (MICH). Sonora: Bavispe, Cañón del Temblar, *E. Phillips 589*, 19–8–1940 (MICH). Jalapa: pr. S. Miguel el Soldado, above Jalapa, *C. Delgadillo et al.*, 8–7–1966 (MEXU). **U.S.A.** Ohio: *Sullivant*, 1850 (JE). Pennsylvania: Philadelphia, *T. James*, 1879 (JE), Misahickon Creek, *G. Kaiser*, 7–12–1911 (DUKE); McKean Co., Quintuple (?), *D. Burnett 2956*, 17–4–1898 (DUKE). South Carolina: Pickens Co., Reedy Cove Falls, pr. Nimmons, *L. Anderson 8856*, 29–8–1949 (DUKE); Oconee Co., Chatooga Rvr. E fork, *L. Anderson 8372*, 18–8–1949 (DUKE). Virginia: Shenandoah Nat. Park, Big Flat Mtn., *I. Schnooberger & F. Wynne*, 26–6–1944 (MICH).

Austria. Panowitzer Wald, pr. Goriziam, *Loitlesberger & Rudez* (C); Meran: Vellanerthal, *Dixon & Nicholson*, Aug 1904 (INA, herb. Luisier). **Italy.** Prov. Cuomo: Borgnana, *A. Artaria*, 13–11–1899 (C, JE); "Gallivago in val Giacomo," *Pfeiffer*, 2–7–1868 (JE); Verbanum, Valle di Bieno, *De Notaris 4953*, 1865 (C, JE); "Luganer See, Cuasso al Piano," *A. Artaria*, 9–5–1897 (C, FH), 9–10–1898, 13–11–1899 (C). Novara: Avola, *L. Calvesi*, Aug 1956 (FI). Piamonte: Lago Maggiore, pr. Mergozzo, *De Notaris*, Aug 1869 (C), Montorfano, *De Notaris* Aug 1859 (FI, RO). **Switzerland.** Ticino: Lugano, *B. Weber*, Apr. 1883 (JE), pr. Lugano, *L. Mari*, 3–10–1889 (JE), "Selva pr. Porya," *L. Mari*, Jul 883, Jul. 1889 (FI); Locarno, *De Notaris 19*, 1863 (R); pr. Locarno, *M. Jäglli*, Apr 1934 (DUKE, JE, MICH).

8. Anomodon sieboldii (Dozy & Molk.) Granzow, comb. nov. *Leptohymenium sieboldii* Dozy & Molk., Ann. Sci. Nat. Bot. sér. 3, 2: 310. 1844. *Neckera sieboldii* (Dozy & Molk.) Müll. Hal., Syn. 2: 81. 1850. *Haplohymenium sieboldii* (Dozy & Molk.) Dozy & Molk., Musci Frond. Arch. Indici 4: 127. 1846.—TYPE: JAPAN. *von Siebold* (holotype: L!, c. fr.).

Haplohymenium brachycladum S. Okamura, Bot. Mag. Tokyo 25: 31. 1911.—TYPE: JAPAN. Hondo, Prov. Ecchu, Tsukiokashin-mura in Kaminiikawa-gun, *Sasaoka*, 9–3–1910 (NICH?).

Haplohymenium okamurae Cardot, Bull. Soc. Bot. Genève, sér. 2, 3: 281. 1911.—TYPE: JAPAN. Shikoku, Tosa, mont Yokogura, *Okamura* (PC).

Haplohymenium gonoi Broth., Öfver. Finsk. Vet. Soc. Förh. 62: 33. 1919–1920.—TYPE: JAPAN. Shikoku, Tosa, *M. Gono 189* (n.v.).

Haplohymenium pellucens Broth., Ann. Bryol. 1: 21. 1928.—TYPE: TAIWAN. Prov. Taihoku, Toihoku, *Sasaoka* (n.v.).

Haplohymenium pinnatum Nog., J. Jap. Bot. 13: 410. 1937.—TYPE: unknown.

Plants delicate and slender, forming lax to rather thick mats, dull brownish green. Branches 0.5–1.5 cm long, 0.3–0.5 mm thick when dry; branching pattern simple, main stem creeping, sparsely branched into prostrate primary branches, which irregularly branch themselves; central strand not differentiated. Leaves julaceous when dry, spreading when moist, delicate, ovate-lanceolate with a very faint constriction above the middle of the leaf, acute; laminal cells inconspicuously pluripapillose; papillae very short, barely branched. Seta 3.5–5 mm. Capsule erect, symmetrical, oblong-ovate; urn 0.7–1.0 (–1.1) mm long, stomata absent; annulus well differentiated, operculum obliquely long-rostrate; exostome ca. 0.26 mm high, smooth below, teeth verrucose; endostome consisting of a basal membrane 3–4 cells high, segments absent. Spores (15–) 17–21 (–23) µm in diameter, densely papillose. Calyptra with thick papillae and hyaline hairs. Chromosome number unknown.

Distribution (Fig. 20). Restricted to Eastern Asia: Japan, Korea, and Taiwan.

REPRESENTATIVE SPECIMENS. **Japan.** Hondo: Prov. Ettyu, Kaminiikawa-gun, *H. Sasaoka*, 30–3–1916 (as *H. brachycladum*, NY). Kyushu: Prov Higo, Aida-m., Kuma-gun, *K. Mayebara 159*, 25–11–1928 (NY); Kagoshima pref., Yakushima Is., Suzukawa, *W. Schofield 53404*, 15–6–1973 (DUKE); Miyazaki pref., Minaminaka obi, *S. Hattori*, Oct 1946 (MICH); Nagasaki *Wichura 1472* (c. fr., NY). **Korea.** Cheju, *Faurie 331*, 1906 (NY). **Taiwan.** "prov. Sintiku: Kyuko," *Y. Simada 341* (as *H. pellucens*, c. fr., NY).

9. Anomodon pseudotristis (Müll. Hal.) Kindb., Enum. Bryin. Exot. 7. 1888. *Hypnum pseudotriste* Müll. Hal., Bot. Zeit. 13: 786. 1855. *Haplohymenium pseudotriste* (Müll. Hal.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907.—TYPE: SOUTH AFRICA. Cape of Good Hope, *Ecklon* (n.v.).

Anomodon filiformis Thw. & Mitt., J. Linn. Soc. Bot. 13: 308. 1873. *Haplohymenium filiforme* (Thw. & Mitt.) Broth., Nat. Pflanzenfam. 1(3): 1236. 1909.—TYPE: SRI LANKA. "Ceylon: Kandy," *Thwaites c256* (holotype: NY!).

Anomodon huttonii Mitt., J. Linn. Soc. Bot. 13: 309. 1873. *Haplohymenium huttonii* (Mitt.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907.—SYNTYPES: NEW ZEALAND. North Island, Great Barrier Isl., *Hutton & Kirk 66 & 144* (MICH! NY!).

Anomodon exilis Mitt., J. Linn. Soc. Bot. 13: 309. 1873.—TYPE: SOUTH AFRICA. Natal, Attercliffe, 1860, *Sanderson* (isotypes: NY-herb. Mitten!).

Anomodon brevinervis Broth., Öfver. Finsk. Vet. Soc. Förh. 33: 107. 1891. *Haplohymenium brevinerve* (Broth.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907.—Type: Australia. Queensland, Helidon, Dec 1888, *Wild 16* (n.v.).

Anomodon mithouardii Paris & Broth., Rev. Bryol. 29: 97. 1902. *Haplohymenium mithouardii* (Paris & Broth.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907.—Type: Vietnam. Entre Lang Son et Dong Dong, Oct. 1901, *Mithouard* (n.v.).

Anomodon submicrophyllus Cardot, Beih. Bot. Centralbl. 19(2): 128. 1905. *Haplohymenium submicrophyllum* (Cardot) Broth., Nat. Pflanzenfam. 1(3): 986. 1907.—Syntypes (n.v.): Taiwan. Maruyama, *Faurie 6 (14, 15)*; Kelung, *Faurie 98*; Tamsui, *Faurie 102, 107*; Hokuto, *Faurie 115* [all in 1903].

Anomodon stenoglossus Cardot & Thér., Bull. Acad. Int. Géogr. Bot. 18: II. 1908.—Type: Japan. Liou-Kiou, Naze, 1898–99, *Ferrié* (n.v.).

Haplohymenium nakajii S. Okamura, J. Coll. Sci. Imp. Univ. Tokyo 36(7): 26. 1915.—Type: Japan. Hondo, Prov. Hoki, Mt. Awashima, 31–10–1913, *Nakaji* (n.v.).

Haplohymenium obsoletinerve Broth., Öfver. Finsk. Vet. Soc. Förh. 62: 32. 1921.—Type: Japan. Hondo, Chiba, *Gono IV.25*. (n.v.)

Haplohymenium pellucens var. *obtusifolium* Broth., Ann. Bryol. 1: 21. 1928.—Type: Taiwan. Prov. Taihoku, Hill Senjyo, *Sasaoka* (n.v.)

Haplohymenium tenerrimum Broth., Rev. Bryol. Lichénol. 2: 10. 1929.—Type: Japan. Prov. Ise, Ujiyamada, *Tutiga* (Herb. Sasaoka, TNS, H?).

Haplohymenium mithouardii var. *viride* Thér., Ann. Crypt. Exot. 5: 179. 1932.—Type: China. Prov. Fukien, Yanping, Buong kang, 23–6–1925, *Chung B.101* (isotypes: MICH! NY!).

Haplohymenium fasciculare Nog., J. Jap. Bot. 13: 791. 1937.—Type: Japan. Sikoku, Mt. Isiduti, prov. Iyo, Aug 1935, *Noguchi 1169* (holotype: HIRO).

Plants dark green to brownish, slender, forming lax, pendulous mats. Branches 0.5–1.5 cm long, 0.3–0.5 mm thick when dry, scarcely branching; central strand not differentiated. Leaves somewhat complanate when moist, delicate, ca. 0.5 mm long, with apex intact, obtuse to rounded; margin entire, not crenulate; costa length variable, from 1/3 to 2/3 of the lamina, covered by laminal cells when reaching beyond the middle; lamina cells pluripapillose, papillae short and inconspicuous, rarely or faintly branching. Seta 2–3 mm long. Capsule erect, symmetrical, oblong–ovate; urn 0.7–1.0 mm long, stomata absent; annulus differentiated; exostome smooth below, teeth verrucose. Calyptra with papillae and hyaline hairs. Chromosome number unknown.

Distribution (Fig. 24). *Anomodon pseudotristis* is rather widely distributed in the regions around the Indian Ocean and the SW Pacific; it is one of the few species that reaches to the Southern Hemisphere: South Africa, New Zealand, probably in Mauritius, SE Asia, including Thailand and Sri Lanka, in addition to eastern Asia (E China, Korea, Japan); also in Hawaii.

Representative Specimens. **South Africa.** Cape Prov.: Groenkop Frst. Resv., *M. & C. Crosby 8080*, 25–1–1973 (DUKE); Transkei, rd. Dwesa to Idutywa, *J. van Rooy 2083* (NY). Natal: St. Lucia Estuary Forest, *J. van Rooy 209* (NY). Transvaal: Marieskop Plantation Natr. Resv., *M. & C. Crosby 7595*, 11–1–1973 (DUKE).

Japan. Honshu: Miyagi Pref., Sendai, *Iishiba*, 16–12–1909 (as *H. triste*, DUKE); Mie Pref., Nabori shi, Akame, *W. Schofield 52214*, 22–10–1972 (DUKE), Shrine naigu, *W. Schofield 52082*, 21–10–1972 (DUKE). Prov. Ettyu, Toyama, *H. Sasaoka 4060*, 6–7–1928 (as *H. sasaokae*, DUKE, MICH, NY). Kyushu: Fukuoka Pref., Nogata, *Y. Kuwahara 2647*, (as *H. sieboldii*, NY); prov. Hyuga, Mt. Aoigadake, *H. Sasaoka 2379,* 26–10–1925 (as *H. submicrophyllum*, NY). **Korea.** Cheju, *Faurie 246* (ex herb. Cardot, as *H. submicrophyllum*, NY). **Thailand.** Udawn, Phu Luanh, *A. Touw 10379,* 7–1–1966 (MICH).

Hawaii. Hawaii: Kohala Mtns., Waipio Valley, Hiilawe Str., *W. Hoe 2399,* 11–6–1972 (as *H. triste*, MICH). Oahu: N. Waianae Mtns, Waialua Distr., Pahole Gulch SW of Peacock Flat, *W. Hoe 2923,* 23–7–1973 (as *H. triste*, MICH).

New Zealand. North Island: N Aukland distr., S of Wangaparaoa Pen., Okura Bush, *J. Beever 21-3,* 1–11–1983 (as *A. huttonii*, MICH). Matakana, *J. Kirk* (as *A. huttonii*, NY).

Anomodon pseudotristis is similar to *A. tristis* but differs in having the leaves of mature branches mostly with a non-fragile, obtuse to rounded apex. Also, the leaf cell papillae are not as prominent as in *A. tristis* or *A. sieboldii*. The names *A. mithouardii* and *A. exilis* have been applied to specimens that seem depauperate or etiolated.

10. Anomodon flagelliformis (Savicz-L.) Granzow, comb. nov. *Haplohymenium flagelliforme* Savicz-L., Bot. Mater. Inst. Sporov. Rast. Glavn. Bot. Sada RSFSR. 1: 98, 101. 1922.—TYPE: RUSSIA. "Asia Orientalis: regio Austro-Ussurensis, in valli fluminis Souczan, pagum Frolovka in flumini Pensaou," 3–8–1913, *Boulavkina* (holotype: LE).

Haplohymenium cristatum Nog., J. Jap. Bot. 20: 146. 1945.—TYPE: unknown.

Plants dark green, very delicate, pendulous; main stem with regular branches, as well as numerous flagelliform ones more than 30 mm long, very slender (less than 0.1 mm in diameter), often branching, bearing much reduced leaves. Stems without a differentiated central strand; pseudoparaphyllia present, foliose but narrow to uniseriate. Leaves oblong-lanceolate, tapering, only slightly constricted above the middle; apex acute to acuminate; costa 0.11–0.19 mm long, extending into the proximal ca. 2/3 of the lamina, cells smooth, covered by lamina cells beyond 1/3–1/2 its length, cell walls thick; margin crenulate, dentate near the apex owing to protruding marginal cells near the apex, smooth at base; laminal cells quadrate to rounded, 6.5–8 µm in diameter, with 4–5 very short to hardly perceptible, non-branching papillae. Perichaetia abundant, present on terminal branches, perichaetial leaves longer than branch leaves but similar to them in areolation and papillae. Sporophytes not seen. Chromosome number unknown.

Distribution (Fig. 20). Restricted to the Russian Far East and Manchuria.

ADDITIONAL SPECIMENS EXAMINED. **Russia.** "Asia Orientalis: in regio austro-ussurensis, in p. sup. fluminis Majche," Sep 1933, *A. Lazarenko* (exicc. Verdoorn, 2 nr. 70, DUKE, MICH, NY).

11. Anomodon longinervis Broth., Hedwigia 38: 243. 1899. *Haplohymenium longinerve* (Broth.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907.—TYPE: JAPAN. Shikoku, Tosa, *Makino* (H-Br).

Anomodon aculeatus Broth. & Paris, Rev. Bryol. 31: 56. 1904.– SYNTYPES (n.v.): JAPAN. Kiu-diu, Ichifusa, Jun 1900, *Faurie 1194*; Tsu-Shima, May 1901, *Faurie 1604*.

Haplohymenium biforme Broth., Bull. Soc. Bot. Genève sér. 2., 3: 281. 1911.—TYPE: JAPAN. Mont Koya, *Nakanishiki* (Herb. Brotherus).

Haplohymenium piliferum Broth. & M. Yasuda, Öfver. Finsk. Vet. Soc. Förh. 62: 33. 1919–1920.—TYPE: JAPAN. Hondo, Mt. Akagi, *Tsunoda* (Herb. Yasuda nr. 34).

Haplohymenium crassum Sakurai, Bot. Mag. Tokyo 47: 337. 1933.—TYPE: JAPAN. Yakushima, *Sakurai 2840* (holotype: TNS).

Haplohymenium spinosum Nog., J. Jap. Bot. 13: 789. 1937.—TYPE: JAPAN. Kyusyu, Ins. Yakusima, prov. Osumi, Jul 1933, *Hasimoto 8640* (holotype: HIRO).

Plants dark green to rusty reddish. Leaves lanceolate, apex acute to obtuse; margin flat, crenulate due to the high papillae; costa extending to near the apex, strong; laminal cells round, bulging, with 1–3 (–4) acute, spinelike high papillae. Perichaetia and perigonia borne at the end of secondary branches. Sporophyte delicate; seta ca. 25 mm long; urn globose, 0.8–0.9 mm long, stomata not seen; exostome yellowish, 0.2 mm high, endostome absent. Calyptra with hyaline hairs. Chromosome number unknown.

Distribution (Fig. 20). Known only from Japan.

REPRESENTATIVE SPECIMENS. **Japan.** Kanto, *E. Iishiba 3045*, 8–8–1911 (DUKE). Honshu: Izushichito Islands, Mt. Hachijo, *T. Osada*, 30–12–1971, *Nakamura*, 3–3–1979 (c. fr. as *H. pseudotriste*, MICH); Gifu pref., Kamo gun, Kashao dani, *M. Mitzutani 16177*, 29–10–1992 (as *H. flagelliforme*, NY); Nagano pref., Kisafukushima, *W. Schofield 51943*, 17–10–1972 (DUKE). Kyushu: Kagoshima pref., Yakushima Is., Onakaido area, *W. Schofield 53526*, 17–6–1973 (DUKE), Korishima, Chuami noike lake, *W. Schofield 52917 & Iwatsuki*, 20–12–1972 (DUKE); Miyazaki pref., Mt. Oyaji, *Z. Iwatsuki & K. Minamidani*, 28–10–1976 (MICH).

The leaf papillae of *A. longinervis* are similar to those of *A. abbreviatus* and *A. solovjovii*, although in *A. longinervis* papillae are more numerous (to 3–4 per cell), not as high, and often branched.

I.c. **Anomodon** section **Thrausti** Granzow, sect. nov.—TYPE: *Anomodon thraustus* Müll. Hal.

Planta tenuis; folia ramealia angusta, tenuia ac/vel fragilia; apex plerumque effractus; costa evanescens, brevis, dimidium laminae vix attingens, subter laminae cellulis occulta.

Plants slender. Secondary branches terete. Branch leaves spreading when moist, delicate, 1.2–1.8 (–2.1) mm long, apex rounded, usually broken off; costa ending well below the apex, extending for 60% the length of the leaf, fading far below the apex or just above the shoulders obscured by laminal cells on its dorsal side. Urn 1.3–1.8 mm long. Calyptra smooth.

12. **Anomodon thraustus** Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 5: 207. 1898.—TYPE: CHINA. "China interior, Shen-si sept., in monte Tuikio-san," Sept 1896, *Giraldi* (holotype: FI!). Fig. 25.

Plants rather slender, in loose mats, dark when dry, bright green when moist; stems creeping, primary branches erect to ascending, julaceous when dry, somewhat densely branched and sometimes irregularly pinnate, with secondary branches to 20 mm long. Central strand of the stem differentiated. Branch leaves slightly crisped when dry, secund, reflexed when moist, rarely complanate, 1.2–1.8 (–2.1) mm long, delicate, abruptly narrowing at the middle from an ovate base to an (often broken-off) obtuse to rounded apex; margin flat, not papillose-crenulate at the insertion. Costa obscured above the shoulders by laminal cells on its dorsal

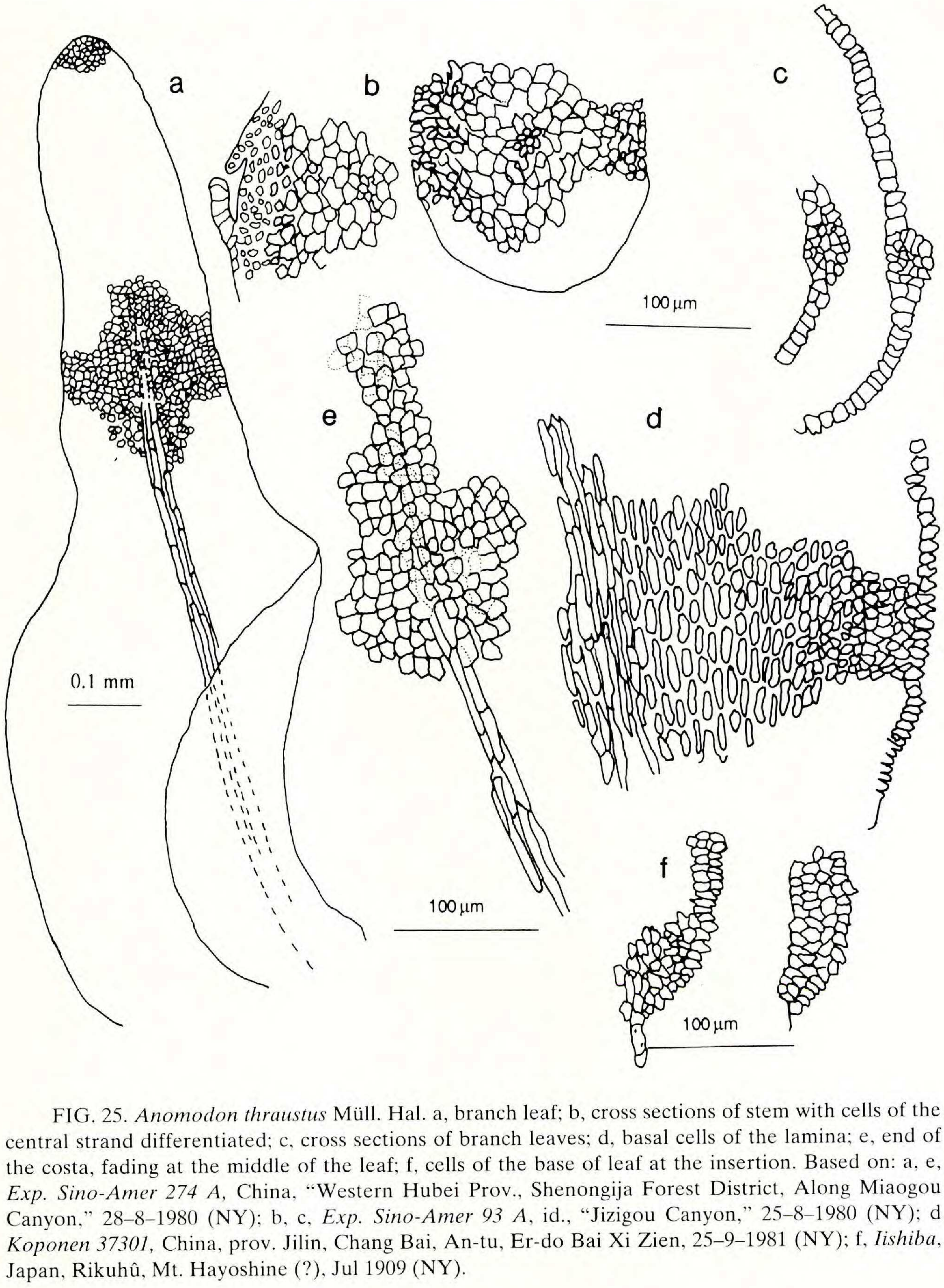


FIG. 25. *Anomodon thraustus* Müll. Hal. a, branch leaf; b, cross sections of stem with cells of the central strand differentiated; c, cross sections of branch leaves; d, basal cells of the lamina; e, end of the costa, fading at the middle of the leaf; f, cells of the base of leaf at the insertion. Based on: a, e, *Exp. Sino-Amer 274 A,* China, "Western Hubei Prov., Shenongija Forest District, Along Miaogou Canyon," 28–8–1980 (NY); b, c, *Exp. Sino-Amer 93 A,* id., "Jizigou Canyon," 25–8–1980 (NY); d *Koponen 37301,* China, prov. Jilin, Chang Bai, An-tu, Er-do Bai Xi Zien, 25–9–1981 (NY); f, *Iishiba,* Japan, Rikuhû, Mt. Hayoshine (?), Jul 1909 (NY).

side, ending far below the apex (more than 15 µm below), often just above the shoulders, occasionally bifid, with in-line large papillae on the dorsal side, where exposed larger than those of the laminal cells; basal pellucid cells extending up to half the basal portion of the lamina, or above; laminal cells with multiple high and branched papillae. Inflorescences on terminal branches, beyond the distalmost branching points. Seta 5–13 mm. Urn 1.3–1.8 mm long, stomata absent, annulus differentiated; operculum short-rostrate, ca. 0.7 mm long. Exostome teeth well developed, ca. 0.3 mm high, papillose to the base; endostome papillose, basal membrane very low (2–3 cells, or ca. 0.045 mm high), with very reduced segments (not more than 0.035 mm long). Spores green, 16–19.5 µm in diameter, finely papillose. Calyptra glabrous. Chromosome number unknown.

Distribution (Figs. 19, 26). Previously, *A. thraustus* has been considered restricted to Japan and eastern China. Gier (1980) cited a specimen from Mexico, and I have also found herbarium material of *A. thraustus* from that country (named as *A. minor*). Its distribution area, therefore, becomes dramatically enlarged. Such disjunction agrees with that of *A. minor*, although in the New World *A. thraustus* occurs more to the south than does *A. minor*.

Additional Specimens Examined. **China.** Heilongjian: "Lesser Khingan Mtns," Shuan-zi-he, *Guo Qian 6672*, 15–7–1963 (NICH). Hubei: Shennongjian Forest distr., Miaogou, *Sino-American Exp. 274A*, 28–9–1980 (as *A. viticulosus*, NY); Jizigou, *Sino-American Exp. 93A*, 25–8–1980 (as *A. minor*, NY). Jilin: "Chang Bai, An-tu, Er-do Bai Xi Zien," *T. Koponen 37301*, 25–9–1981 (as *A. minor* subsp. *integerrimus*, NY); Jian, Dayu shan, *Guo Qian 7802*, 8–9–1963 (as *A. rugelii*, IFSBH); Wang Qing Xian "Wang-chiu," Daxinancha, Nangou, *Guo Qian 8575*, 16–8–1973 (IFSBH). Tibet: Ya-Dong, *Zang Mu 56*, 29–5–1975 (NICH). **India.** Himachal Pradesh: Simla "7000," *T. Thomson 1172*, 1847 (as *A. obtusifolius* var., *Wils*., syntype for *A. integerrimus*, NY-herb. Mitten), Simla "7000, 8000," *T. Thomson 1126*, Oct 1849 (mixed with syntype of *A. planatus*, herb. Mitten, NY). Kumaon: Dahli valley, *J. Duthie 6359*, 7–8–1886 (as *A. planatus*, MICH). Uttar Pradesh: "Western Hymalaya, Seven Oaks estate," Mussoorie, *W. Gollman*, 2–10–1900 (as *A. glossophyllus*, NY). "India Oriental," *Bell 187* (as *A. integerrimus*, NY). **Japan.** Honshu: Hiroshima pref., Tojo-cho, Taishaku, *M. Higuchi*, 7–10–1978 (HIRO); Iwate pref., Rikuchu: Mt. Hayachine, *E. Iishiba*, Jul 1909 (as *A. minor*, NY). **Korea.** Keisyo nando, Mitsuyo, *N. Maki 2985*, 31–7–1931 (NICH); *Sauer*, 1924 (as *A. minor*, JE); Mt. Ciak, *W. Hong 5874*, 16/17–7–1961 (as *A. integerrimus*, NICH); Mt. Sokri, *W. Hong 2801*, 21–12–1960. Fusan, *Faurie 241*, 1906 (ex herb. Cardot NY). **Nepal.** "In Himalayae reg. temp.," *Wallich* (mixed with type for *A. integerrimus*, herb. Mitten, NY). **Russia.** Far East (Primorsk) : Ussuriisk, rvr. Suputinka, *L. Bardunov*, 6–9–1962 (NICH), ibid., *V. Ardeieva*, 3–9–1968 (NICH), Tetjukhe, *L. Bardunov*, 29–11–1961 (NICH), pr. Partizansk, *L. Bardunov & V. Tchardantzeva*, 16–9–1964 (NICH), Schkotovskyi, pr. Podiapolsk, *L. Bardunov*, 9–9–1974 (NICH); "regio Ussuriensis," Vladivostok, *P. Sinzer*, 25–04–1905 (as *A. minor*, ex herb. Brotherus FI), Nikolok, *P. Sinzer*, 3/1905 (as *A. minor*, FH), Utsisheibo (Manchuria), Vladivostok, *P. Sinzer*, 13–03–1905 (as *A. minor*, c. fr., ex herb. Brotherus FI); "Far East, Lake Khanka, pr. village of Lusanovo," *L. Bardunov*, 23–8–1962 (NICH); "Sibiria: Primorskaja, Okaenskaja," *E. Sinova*, Sep 1926 (as *A. minor*, MICH).

Mexico. Hidalgo: Jacobo, *V. Chase 7405*, 11–7–1939 (Bartram herb. FH). Jalisco: Slopes of La Ferrería, above Manantlán, *H. Crum 914, 926a, 942*, Jul 1949 (as *A. minor*, MICH). San Luis Potosí: 45 km E Río Verde, betw. Ciudad Valles and S. Luis Potosí, *C. Delgadillo*, 4–12–1978 (as *A. minor*, MEXU).

Anomodon thraustus has often been reduced to synonymy within *A. minor*; however, Sakurai (1954), Iwatsuki (1963), Iwatsuki and Noguchi (1973), Noguchi (1974) and other Japanese authors recognize it as a species. Unquestionably, *A. thraustus* is closely related to *A. minor*, but they differ, in addition to the more delicate habit of *A. thraustus*, in the following foliar characters. 1)The leaves of *A. thraustus* are almost invariably not complanate when moist but clearly reflexed, spreading in all directions. 2)The costa is short and entirely obscured by laminal cells beyond the shoulders, ca. 1/3 from the apex. 3)The leaf apices are often broken off, as in *A. tristis* or *A. dentatus*. 4)The cells are papillose-crenulate at the insertion, almost spinulose, in *A. minor* but entire in *A. thraustus*. Also, the central strand of the stem is differentiated in *A. thraustus*, but not in *A. minor*. The exostome is made of well-developed and regular teeth, and the endostome is papillose with segments ca. 3 cells high in *A. thraustus*, whereas in *A. minor* teeth of the exostome are irregular, and the endostome is smooth and practically without segments.

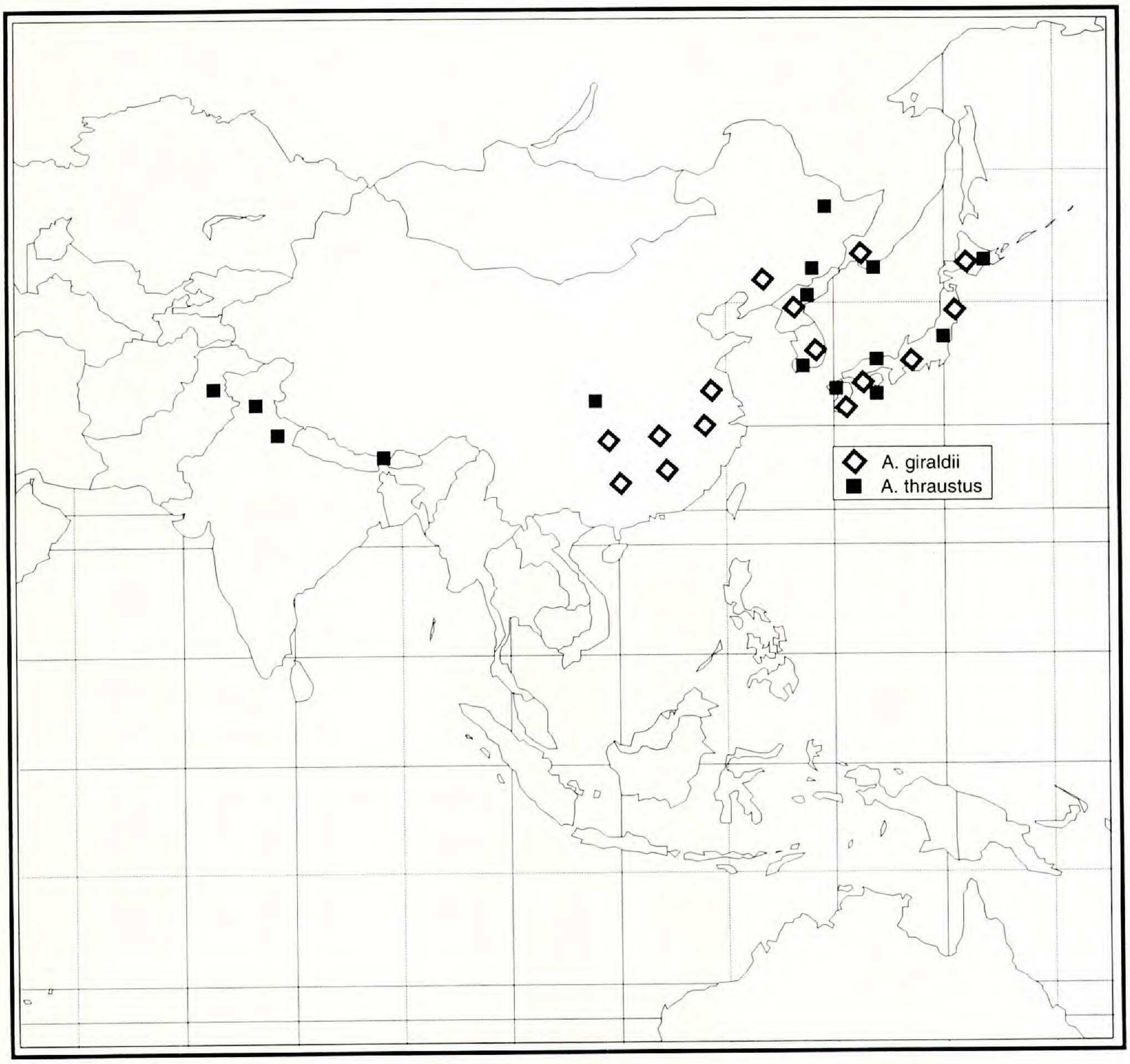


FIG. 26. Distribution of *Anomodon giraldii* and *A. thraustus* in central and eastern Asia.

Further confusion resulted from Mitten's having specimens of *A. thraustus* mixed with his type material for *A. integerrimus* and *A. planatus* (lectotype for *A. integerrimus*: Nepal, *Wallich*, Mitten Herbarium, NY; lectotype for *A. planatus*: Simla, *1126*, 10/49, "*A. obtusifolius* small barren state W." Mitten Herbarium, NY, here designated). His protologues for these two taxa do not describe the morphology of *A. thraustus*, nor do the sketches of leaves drawn on the herbarium packets containing the syntypes of *A. integerrimus* and *A. planatus* depict the leaves of *A. thraustus* but rather those of *A. minor*. *Anomodon integerrimus* and *A. planatus* are synonyms of *A. minor*, not of *A. thraustus*. Mitten's mixed types are probably the cause of much of the confusion surrounding the identity of both taxa.

II. Anomodon subgenus **Pseudoanomodon** Limpr., Laubm. Deutschl. 2: 774. 1895.—TYPE: *Anomodon attenuatus* (Hedw.) Hüb.

Stems and primary branches branching in a stairway fashion, or with secondary branches irregularly pinnate, profusely fasciculate. Leaf apex acute to acuminate; laminal cells rhombic in most taxa.

13. Anomodon rostratus (Hedw.) Schimp., Syn. Musc. Eur. 448. 1860. *Leskea rostrata* Hedw., Sp. Musc. 226. 1801. *Hypnum rostratum* (Hew.) P.-Beauv., Prodr. 69. 1805.—TYPE: U.S.A. "circa Lancaster, Pensylvaniae," *Muhlenberg* (holotype: G -herb. Hedw. Schwaegr.!). Fig. 27.

Plants forming thick dense mats, glaucous, light to dull yellowish green. Stems prostrate, profusely branching, with primary branches 0.5–2 cm long, ca. 1.0 mm thick when dry, clustered, with a fasciculate, pseudo-verticillate branching pattern, secondary branches erect, stem with a differentiated central strand of smaller cells, pseudoparaphyllia absent. Branch leaves julaceous, imbricate when dry, erect when moist; leaves ovate-lanceolate, acuminate, slightly constricted in the distal 1/3, up to 1.2 mm long, margins revolute, ending in a hyaline hair-point several cells long (to 0.2 mm or more) and one cell thick; costa pellucid, ending well below the apex, ca. 10 µm, often somewhat flexuose above, with high papillae in one line at the back, sometimes slightly branched, almost scabrid at the base, the group of basal cells small, very few, with sinuose walls; medial laminal cells rhomboidal, scarcely isodiametric at the basal 1/2–2/3 of the lamina, multipapillose, with papillae slightly branched. Perichaetial buds beyond the last branching nodes; perichaetial leaves elongate, long-acuminate, smooth. Seta dark red, 7–13 mm long, sometimes shorter. Capsule short, elliptic; urn 1–1.5 mm long, ovoid to oval-cylindrical, with stomata at the base, annulus of 2 rows of cells; operculum obliquely rostrate, 0.8–1.1 mm long; peristome well developed, exostome 0.2–0.3 mm high, teeth trabeculate, with a yellowish base, striolate to the middle or more, apex conspicuously papillose; endostome well developed, with tall basal membrane, 7 cells high or more, as high as the exostome, segments keeled, long and slender, 0.9–1.1 mm high, papillose; cilia absent. Spores 11.5–15 µm in diameter, densely papillose. Chromosome number: $n = 10 + x/y$ (in meiosis, North Carolina: Granzow-de la Cerda 1988b). Additional illustrations in Crum and Anderson (1981) and Schumacker et al. (1982).

Distribution (Figs. 15, 18, 28). Circumboreal montane, from central Europe south to the Pyrenees and Italian Alps, east to the Caucasus; widely distributed throughout eastern North America, from Newfoundland to Mexico and Guatemala, also in Bermuda, Hispaniola, and Jamaica. Iwatsuki (1963) excluded this species from Japan and, in general, from eastern Asia, given that most records are misidentifications of *A. longifolius* (Yano 1957) or *Claopodium pellucinerve* (Reimers 1936). *Anomodon rostratus* usually grows in deciduous forests, sometimes in rather open spaces, as well as secondary forests, where it forms dense and thick mats, often very extensively, on vertical rocks, calcareous in Europe (Schumacker et al. 1982) but also acidic in North America. In the eastern United States, it is almost always found at the base of deciduous trees or on their bark, on soil, and, less often, on fallen logs.

REPRESENTATIVE SPECIMENS. **Georgia.** Tzenis Tzchali rvr., "Svania Dadianosum, Hippi, inter Muri et Lentechi," *Sommier & Levier*, 29–7–1890 (NY).

Canada. British Columbia: Eagle Pass Mtns., Big Eddy of Columbia Rvr., nr. Revelstoke, *W. Taylor 5310*, 11–8–1921 (MICH). New Brunswick: Albert Co., Fundy Nat. Park, Dickson Falls, *R. Ireland 10744*, 2–7–1967 (MICH). Newfounland: Notre Dame Bay, New World Isl., Cobbs Arm, *G. Brassard 10506 et al.*, 19–10–1975 (NY). St. Barbe S Distr. SE of Parsons Pond, *J. Hancock & C. Butler 468*, 3–7–1972 (MICH). Nova Scotia: Colchester Co., Five Islands, *R. Ireland 17222*, 10–7–1974 (MICH). Ontario: Grey Co., Inglis Falls, nr. Owen Sound, *H. Crum* 11027, 3–8–1961 (MICH). Ottawa Co., *J. Macoun*, 20–10–1893. Manitoulin Isl., Tamarack Point, *C. Grassl 6219*, 19–7–1932 (MICH).

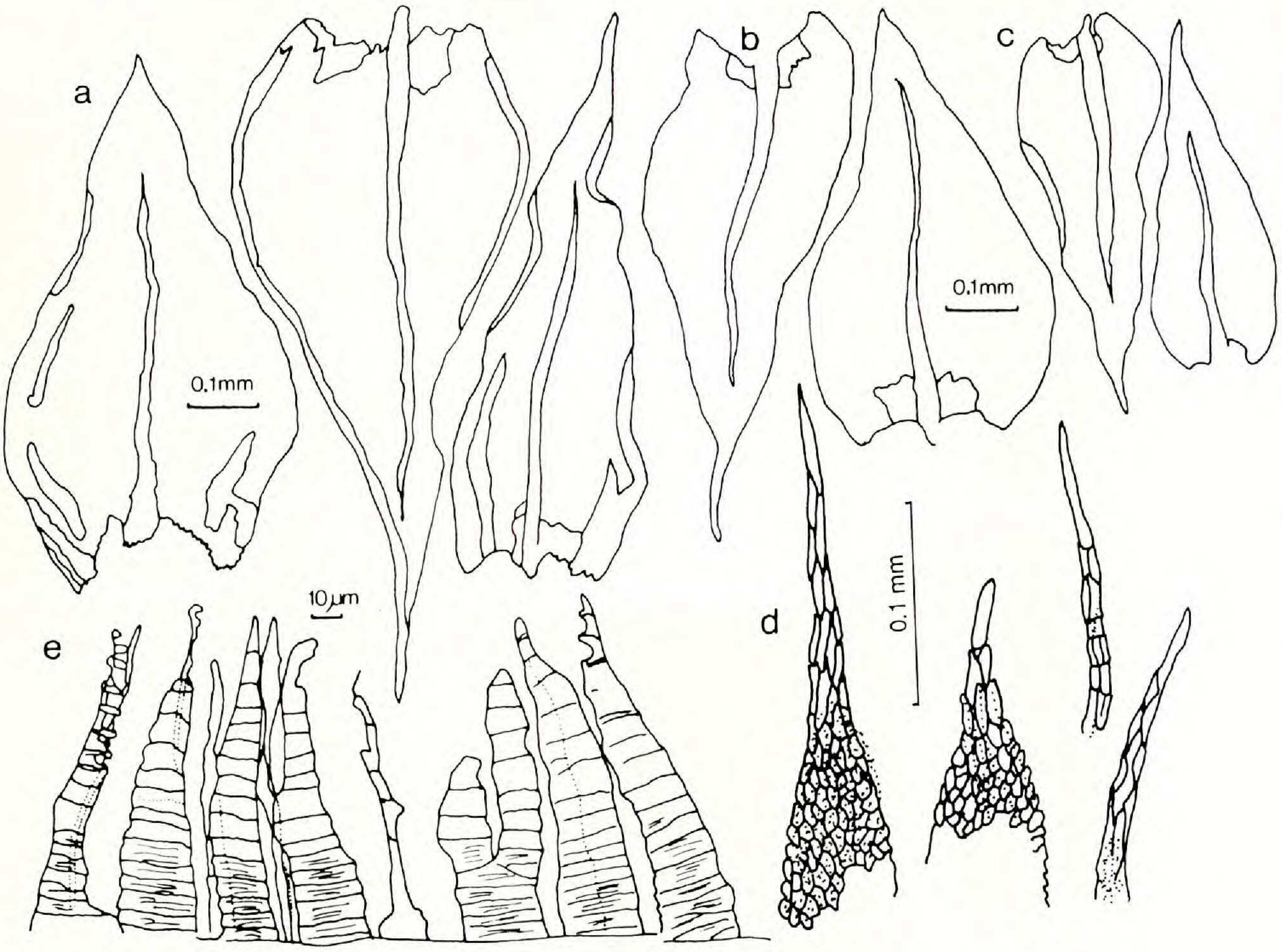


FIG. 27. *Anomodon rostratus* (Hedw.) Schimp. a–c, branch leaves; d, apex of branch leaves; e, portion of peristome. Based on: a, d, e, *F. Artaria*, Italy, Como prov., Bucca del Pertuso, Blevio, 15–7–1897 (NY); b, *Hermann 26045*, Mexico, Nuevo León, Monterrey, Sierra Madre Oriental, 22–7–1975 (NY); c, *Boros*, Hungary, "Comit. Veszprém, rivi Gerence, pr. Baconybél," 3–4–1959 (NY).

Québec: Armand, S of Montreal, *K. Holmen*, 24–9–1959 (NY). Gaspé Sud, Percé, *H. Crum & H. Williams 10882*, 25–7–1960 (MICH). **Guatemala.** Alta Verapaz: Río Carchá, entre Cobán y S. Pedro Cobán, *P. Standley 90129*, 26–3–1941 (herb. Bartram FH), *90130* (MICH). El Quiché: *A. Sharp 2434*, 6–2–1945 (herb. Bartram FH). **Mexico.** Chiapas: Las Casas, *A. Sharp 3521*, 25–4–1945 (US, MICH, NY); S of San Cristóbal, *R. Düll 16*, 8–10–1966 (NY). Hidalgo: Chapulhuacán, *A. Sharp 1541a, 1542a, 1580*, 7/8–12–1944 (DUKE, MICH, NY, US); Jacala, *A. Sharp*, 17–12–1962 (US). Nuevo León: Sierra Madre Oriental, Monterrey, Chipinque, *F. Hermann 26043*, 2–7–1975 (NY), *26037b*, 27–1–1975 (MICH); Sierra Madre, Monterrey, *C. Pringle 10460*, 29–5–1908 (JE, US). Puebla: pr. Zacapaxtla, *A. Sharp 4185*, 17–10–1945 (MICH). San Luis Potosí: "above Xilitlá," *A. Sharp 5866, 5868*, 21–4–1946 (MICH, NY, US). Tamaulipas: Sierra Madre, W of Victoria, *H. Crum 1831*, Aug 1950 (US). Jalapa: Acutlzingo, pr. El Puerto, *A. Sharp 629, 670*, 6/13–9–1944 (MICH). **U.S.A.** Alabama: Madison Co., Monte Santo Co., *T. Bryson 898*, 3–1–1976 (MICH). Arizona: Sta. Cruz Co., Sta. Rita Mtns., White House Canyon, *I. Haring 3472 & H. Haskell*, 7–5–1945 (MICH). Arkansas: Drew Co., Wilmar, *D. Demaree 24239*, 10–4–1943 (MICH). Colorado: Chandler Canyon, *T. Brandegee*, 1876 (NY). Montrose Co., W Paradox Creek, *W. Weber et al. B-43564*, 1–6–1973 (NY). Connecticut: East Haven, *J. Allen*, 7–9–1882 (MICH). Florida: Jackson Co., Marianna Caverns, *R. Schornherst 1508*, 9–3–1940 (MICH). Georgia: Stone Mtn., *J. Small*, Jan 1894 (MICH); Demorest, *O. VanHilse*, Feb 1913 (MICH). Illinois: Pope Co., Bell Smith Springs, NW of Eddyville, *D. Vitt 7407*, 25–5–1973 (MICH). Iowa: Fayette Co., Brush Creek Canyon St. Park, *S. Gradstein & D. Horton 6392*, 16–4–1987 (MICH). Kansas: Douglas Co., 14 km S-SE of Lawrence, *S. Churchill 9370*, 11–4–1978 (MICH). Riley Co., 14 km SW of Manhattan, *S. Churchill 9401*, 14–4–1978 (MICH). Kentucky: Trigg Co., Cadiz Mill, *A. Harvill 2000*, 10–8–1946 (MICH). Maine: Somerset Co., Moxie Falls, *B. Allen 9327*, 11–7–1990 (MICH). Massachusetts: Weston, *J. Lowe*, 24–12–1903 (DUKE); Worcester Co., Bolton, *H. Greenwood 155*, 3–6–1933 (DUKE). Michigan: Cheboygan Co., Mill Creek, *N. Shiskoff 10-33*, 11–7–1980 (MICH). Huron Co., Port Austin, *I. Schnooberger 1754*, 8–10–1938 (MICH). Marquette Co., Presque Isl., *F. Hermann*

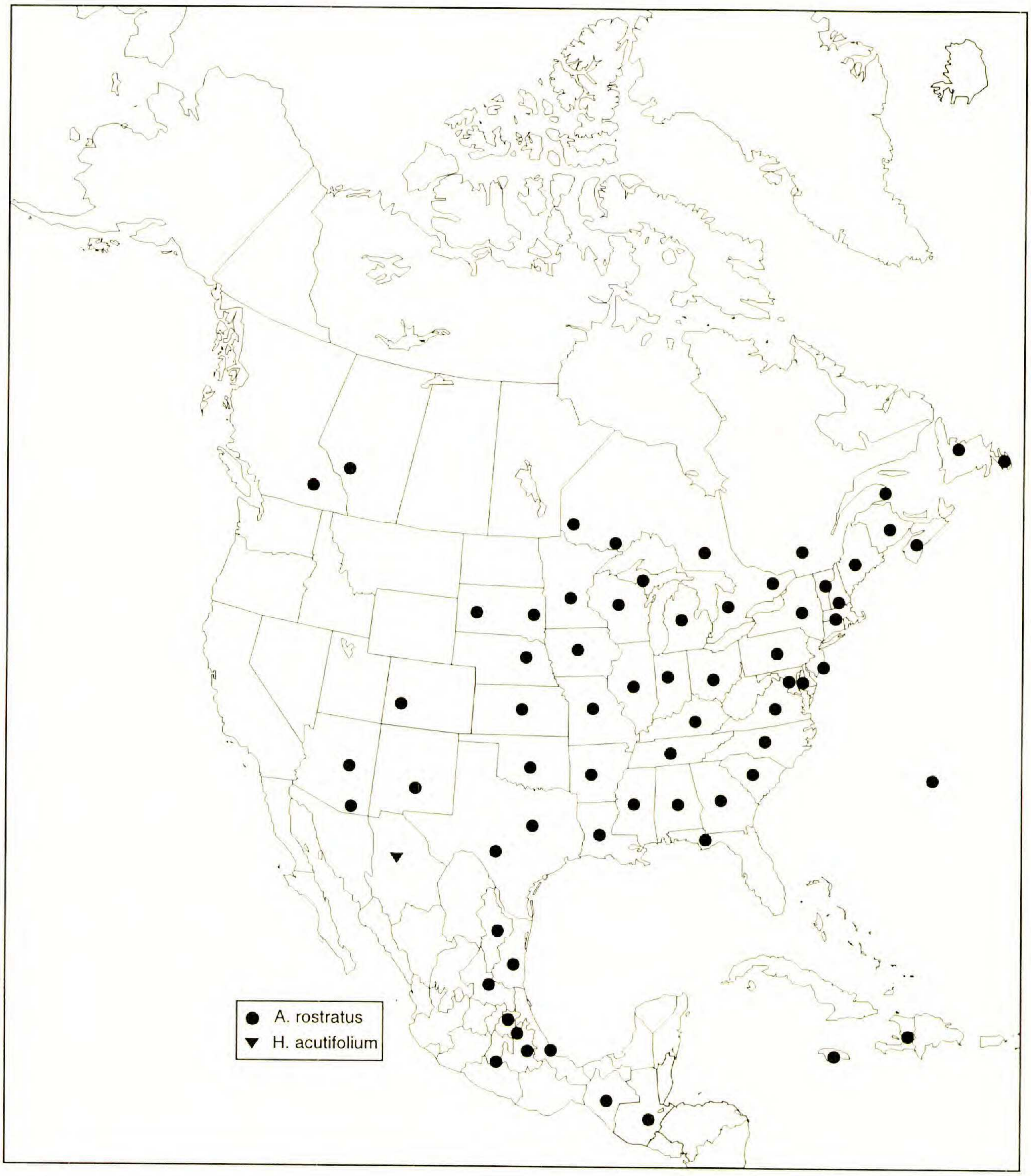


FIG. 28. Distribution of *Anomodon rostratus* and *Herpetineuron acutifolium* in the New World.

28757, 4–10–1978 (MICH). Missouri: Valley View Glades St. Nat. Area, *A. Whittemore 3408 et al.*, 12–3–1989 (MICH). Nebraska: Cass Co., Weeping Water, *J. Sheldon B25*, 29–8–1898 (NY). New York: Clinton Co., Valcour Isl., *J. Smith 38084 & L. Lowinger*, 10–6–1965 (MICH). Suffolk Co., L.I., Peconic, *R. Latham 36740*, 25–3–1947 (MICH). North Carolina: Macon Co., Chatooga River, *I. G.-de la Cerda 1321*, 16–6–1984 (DUKE); Orange Co., New Hope Creek, *I. G.-de la Cerda 1939*, 3–11–1984 (c. fr., DUKE); Wake Co., Neuse River, Wake Forest, *L. Anderson 11159*, 23–11–1959 (c. fr., DUKE); Chowan Co., Edenton airport, Albermale Sound, *A. Weakley 3540-3549*, 21–11–1983 (c. fr., DUKE). South Carolina: Berkeley Co., Cypress Gdns. *E. Taylor 2211*, 7–4–1960 (NY). South Dakota: Lawrence Co., Black Hills, Spearfish Canyon, *E. Lawton 2177*, 29–9–1953 (NY). Meade Co., Black Hills, Stagebarn canyon area, *S. Churchill 9216*, 26–5–1977 (MICH). Tennessee: Wayne Co., Glenrock Branch, *L. Timme 8839 & L. Jackson*, 20–1–1989 (MICH). Sevier Co., Elkmont, *A. Sharp 405*, 25–2–1940 (MICH). Texas: Dallas Co., nr. Dallas, *J. Boll*, 1874–80 (NY). Liberty Co., 21 mi SE of Cleveland, *G. Webster & R. Wilbur 668*, 3–7–1959 (MICH, NY). Virginia: Smyth Co., Mount Jefferson Natl. Forest, *I. G.-de la Cerda 1887*, 6–10–1984 (c. fr., DUKE). West Virginia: Greenbrier Co., S of White Sulphur Springs, *L. Anderson 24752*, 16–7–1986 (DUKE). Wisconsin: Richland Co., Richland Ctr., *M. Nee 12537*, 4–7–1974 (MICH).

Bermuda. Harrington House, *S. Brown 558* (NY). Abbots cliff: *E. G. Britton 1877*, 13–9–1813 (US). **Haiti.** Mtns above Kenskoff, *F. Mackaness 153*, 19–1–1944 (MICH); btw. Savanne Zombi and Satnon, *F. Mackaness 70*, 18–3–1944 (MICH). Dept. de Sud'est: Massif de la Salle, *W. R. Buck 9347*, 21–11–1982 (NY). **Jamaica.** Abbey Green: *W. Maxon 10061*, Jul 1926 (NY); vicinity of Arntully, *Orcutt 3185*, 3–10–1927 (herb. Bartram FH); vicinity of Abbey Green, *W. Maxon 10083*, Jul 1926 (US). Blue Mountains: *G. Orcutt 2854*, 5–9–1927 (US, FH). "Westhalia: (Ceddar Hurst)," *C. Orcutt 3762*, 1–11–1927 (US).

Austria. Baden: Wien, *J. Benoger (?)*, 1871 (NY). Salzburg, *D. Sauter* (NY). Tirol: Merau, *Milde* (NY). "Austria inferor": Isaden (?), *Juratzka*, 30–6–1867 (NY). "Niederösterreich": *Baumgartner*, 30–4–1891 (NY). **France.** Haute-Garonne: Prat de Joueou, "énvirons de Luchon," *Dismier 281*, 14–8–1928 (MA). **Germany.** Bayern: "Nagelfluh, pr. Shäfflarn," *Molendo*, 1860 (NY), *I. Familler*, Aug 1906 (MICH). **Hungary.** Comit Veszprém: "rivi Gerence, pr. Bakonybél," *A. Boros*, 3–4–1954 (NY), Nagy-Pénzlik cave, mt. Somhegy, *A. Boros*, 4–10–1937 (MICH). **Italy.** Como: Buca del Pertuso, Blevio, *F. Artaria*, 15–7–1897 (NY); "Nino, inter Blevio et Como," *F. Artaria*, 20–9–1897 (NY). **Romania.** Transylvania: distr. Fàgàras, *M. Péterfi*, 10–8–1921 (NY). **Spain.** Girona: vall de Vidrà, Les Llances, *I. G.-de la Cerda 2323a & M. Sanz*, 10–1–87 (c. fr., BCB, MA), Rec de l'Espirau, *M. Sanz*, 7–3–1986 (BCB), Vilallonga de Ter, *F. Lloret 33.3.7*, 13–3–1986 (BCB). Huesca: Ordesa, *R. Düll*, 23–5–1960 (BCB) (see Granzow-de la Cerda, 1988a). **Switzerland.** Ticino: Lugano, Gandria, 17–9–1885 (c. fr., ex herb. Boissier NY); Campione-Bissone, *P. Conti*, Oct. 1893 (MICH).

Anomodon rostratus is well distinguished from all others in the genus by having the shortest branch leaves, ending in a hair point. The leaf areolation is also more lax; the basal portion of rhomboidal cells extends beyond half the leaf length. The species somewhat resembles *A. longifolius* in having long, acuminate leaves with revolute margins. Nonetheless, differences between both species are more than obvious: *A. rostratus* has leaf cells with multiple papillae, a uniseriate acumen throughout most of its length (or biseriate at the base) with cells completely distinct from those of the lamina (i.e., hyaline and much longer than wide). Also, *A. longifolius*, along with *A. rugelii*, are the only species that have pseudoparaphyllia.

Anomodon rostratus fruits profusely in North America, but mostly remains sterile in Europe, although a specimen bearing two sporophytes was found in a population from NE Spain (Granzow-de la Cerda 1988a). Based on observations by Schumacker et al. (1982), it can be inferred that these are the only sporophytes ever reported from Europe. According to those authors, the absence of sporophytes is due to the absence of male gametophytes in Europe. My observations revealed that in North America male gametophytes are extremely scarce, even in populations with abundant sporophytes (Granzow-de la Cerda 1988b, 1989b).

Iwatsuki stated that *A. rostratus* var. *japonicus* Sak. belongs to *Trachypus humilis* (Iwatsuki 1963: 58).

14. Anomodon attenuatus (Hedw.) Hüb., Musc. Germ. 562. 1833. *Leskea attenuata* Hedw., Spec. Musc. 230. 1801. *Hypnum attenuatum* (Hedw.) Sm., Fl. Brit. 3: 1279. 1804.—TYPE: GERMANY, sine loc., c. fr. (syntypes: G-herb. Hedw.-Schwaegr.!). Fig. 17c–e.

Hypnum fulvum Brid., Musc. Rec. 2(2): 188. 1801. *Hypnum attenuatum* var. *fulvum* (Brid.) Steud., Nomencl. Bot. 2: 252. 1824.—TYPE: Herb. Ph. Commerson (not located).

Anomodon wrightii Müll. Hal., Hedwigia 37: 262. 1898.—TYPE: CUBA. "Rocks in a ravine," *Wright* (isotypes: in Cuban Mosses exicc. nr. 69, MICH! NY!).

Plants forming dense mats, dull yellowish green. Primary branches 1.5–3 cm long, 0.8–1 mm thick when dry, prostrate to arcuate, irregularly pinnate, secund when dry, complanate when wet, mostly attenuate, branching pattern often consisting of several orders of successive branching, in a stepwise fashion; without a differentiated central strand, pseudoparaphyllia absent. Branch leaves slightly narrowed at the middle, with the portion above the constriction mostly lanceolate, acute, sometimes obtuse or slightly apiculate, 1.2–2 (–2.2) mm long; margins flat, entire from the base up (although cells moderately mammillose at the insertion); apex sometimes denticulate, with cells at the tip, along the margins, generally hyaline and somewhat larger and less papillose than the laminal ones; costa pellucid, abruptly ending a few cells below the apex, sometimes fading in youngest leaves; cells on back of costa usually less than 23 µm long, sometimes up to 35 µm long; hyaline basal cells poorly differentiated, sometimes chlorophyllose, but extending more than half the length of leaf base; cell walls somewhat sinuose, porous near the costa; upper laminal cells quadrate, 6–8 µm, pluripapillose, papillae branched. Perichaetial buds never present beyond the last branching points; perichaetial leaves abruptly narrowed, costa reaching well into the distal half of lamina, ending near the apex in the innermost leaves. Seta 10–15 mm. Urn 1.6–2.8 mm long, with stomata at the base; annulus not differentiated; operculum obliquely short-rostrate, ca. 1.3 mm long; exostome striolate below, teeth irregular, 0.35 mm high, yellow, becoming white with age, trabeculate and more or less finely papillose toward the apex; endostome also papillose with high basal membrane (3–4 cells high), segments keeled and well developed, to 0.03 mm long, cilia absent. Spores 10–13 µm in diameter, densely papillose. Chromosome number: $n = 10 + x/y$ (in meiosis, North Carolina: Granzow-de la Cerda, 1988b).

Distribution (Figs. 12, 13, 15, 20). Present throughout Europe (except in Ireland, Portugal, and the Mediterranean islands), Turkey, and from the Caucasus to Kashmir; very abundant in eastern and midwestern North America, from Newfoundland to Manitoba, south to Florida, Mexico, Guatemala, and Belize; Cuba, Jamaica, and Hispaniola. *Anomodon attenuatus* grows on bark, mostly at the base of trees, and also on soil and rocks. Populations in North America produce sporophytes abundantly.

REPRESENTATIVE SPECIMENS. **India.** Kashmir: Ferozenpur Nullah, Gulmarg, *R. R. Stewart 10572a*, 2–9–1929 (NY). **Russia.** Krasnodorskyi: Teberda, *Abramov*, 21–8–1955 (NY).

Canada. New Brunswick: Restigouche Co., St. Jean-Baptiste-de-Restigouche, *R. Ireland 14478*, 14–8–1970 (MICH). Newfoundland: St. Barbe, Doctor's Hill, *R. Tuomikoski 4618*, 29–7–1948 (MICH); Humber, Benoit's Rvr., *R. Tuomikoski 5412*, 15–8–1949 (MICH). Nova Scotia: Annapolis Co., E shore of Kejimkujik Lake, *R. Ireland 12554*, 3–8–1968 (MICH); Cumberland Co., Wentworth, *R. Ireland 10681*, 7–9–1967 (MICH). Ontario: Grey Co., Sydenham Rvr., Inglis Falls, *H. Crum 11034*, 3–8–1961 (MICH); Lake Superior, Thunder Bay District, *W. B. Schofield 27244*, 1–7–1965 (as *A. minor*, DUKE), W. end of Albert Lake, *C. Garton 14878*, 18–4–1972 (MICH). Québec: Pontiac Co., SE corner of Parc de la Vérendrye, *R. Ireland 16125 & T. Koponen*, 15–6–1972 (MICH). **Guatemala.** Alta Verapaz: Río Carchá, pr. San Pedro Carchá, *P. Standley 92104*, 12–4–1941 (NY, MICH). Baja Verapaz: pr. Patal, *A. Sharp 2947*, 3–3–1945 (MEXU). El Quiché: Neboj, *A. Sharp 2429*, 6–2–1945 (MEXU, US). **Jamaica.** Arntully, *C. R. Orcutt 3840*, 12–11–1927 (DUKE). **Mexico.** Chiapas: San José del Lago, *A. Sharp 3572*, 3–5–1945 (US); "Las Casas," *A. Sharp 3516*, 26–4–1945 (MEXU, NY); "Strasse Ocosingo," San Cristóbal, *Eggers & Frahm 29*, 10–3–1979 (NY). Durango: El Salto, *A. Sharp 1889*, 31–12–1944 (MICH). Hidalgo: Chapulhuacán, *E. Frye 2874a* (MICH). Nuevo León: Hacienda Vistahermosa, 35 mi S of Monterrey, *L. Harvey 1052, 1055*, 25–6–1939 (MICH). Oaxaca: pr. S. Pablo Ayutla, *A. Sharp et al.*, 23–12–1972 (MEXU). Puebla: Río Necaxa, pr. Huachinango, *A. Sharp 3143*, 27–3–1945 (MICH). San Luis Potosí: Xilitlá, *A. Sharp 5836*, 21–4–1946 (US), *C. Delgadillo et al.*, 17–12–1976 (MEXU). Sonora: Bavispe, Cañón del Temblar, *E. Phillips 596*, 19–8–1940 (MICH). Tamaulipas: pr. Rancho del Cielo, Gómez Farías, *C. Delgadillo*, 1–5–1967, ibid. *A. Sharp*, 1–8–1974 (MEXU). Jalapa: "19 km NW Jalapa," *W. Rauh & R. Düll 31*, 15–10–1966 (JE); NW of Caotepec, pr. Consolapán, *L. Gil Juárez 60*, 23–5–1975 (NY); "Strasse Orizaba-Tehuacán," *Eggers & Frahm 38*, 23–3–1979 (NY). **U.S.A.** Alabama: Hale Co., Rock Hollow, Havana P.O., *H. Wagner et al. 71167*, 30–12–1971 (MICH). Arizona: Apache Co., Apache Reservation, *W. Phillips*, 2–9–1949 (DUKE, MICH).

Arkansas: Newton Co., Little Buffalo Rvr., *L. Anderson 11969*, 29–5–1953 (DUKE, MICH). Colorado: Boulder Co., Boulder Canyon, *W. Weber*, 30–3–1963 (MA). Connecticut: Valley Forge, Upper Glen, *W. Stair & W. Allen*, 17–6–1939 (MICH). Georgia: Stephen Co., Toccoa Falls, *R. Lampton 1804*, 15–5–1965 (MICH). Illinois: LaSalle Co., French Canyon, Starved Rock, *W. Hinton*, Apr 1970 (MICH). Indiana: Turkey Run Hollow, *D. Richards et al. 5896*, 23–11–1947 (MICH). Kansas: Doniphan Co., Missouri Rvr., *S. Churchill 10860*, 30–6–1979 (MICH). Louisiana: Natchitoches Par., Cunningham Brake, *J. Bruza 643*, 3–3–1978 (MICH). Maryland: Prince Georges Co., Beltsville, Paint Branch, *F. Hermann 16414*, 27–11–1960 (MICH). Massachussets: Amherst (as *A. viticulosus*, FH). Michigan: Mackinac Co., Caffey Corner, *H. Crum*, 9–8–1968 (MICH); Washtenaw Co., Cascade Glen, *G. Webster 577*, 2–5–1959 (MICH). Mississippi: Scott Co., *K. Rogers 9357*, Jan 1974 (MICH). Missouri: Barry Co., 2 mi N of Eagle Rock, *P. Redfearn 26059*, 4–5–1969 (as *A. viticulosus*, MICH); Franklin Co., Meramec Rvr., *B. Allen 6108*, 30–1–1988 (MICH). Minnesota: Goodhue Co., *B. Johnson*, 3–5–1953 (MICH). New York: Columbia Co., Old Chatham, *S. Smith 3119 & B. Reilly*, 15–5–1961 (MICH). North Carolina: Transylvania Co., Horsepasture River, *I. G.-de la Cerda 1938*, 31–11–1984, *1286*, 13–6–1984 (DUKE); Graham Co., Joyce Kilmer Mem. Park, *I. G.-de la Cerda & K. Renzaglia*, 3–10–1987 (c. fr., DUKE); Macon Co., *I. G.-de la Cerda 1236*, 8–6–1984 (DUKE), Nantahela River headwaters, *I. G.-de la Cerda 1260*, 11–6–1984 (DUKE), Crow Creek, *I. G.-de la Cerda 1399*. 19–6–1984 (DUKE); Orange Co., Eno River St. Park, *I. G.-de la Cerda 1999,* Mar 1985 (DUKE). Pennsylvania: Hungtindon Co., Spruce Creek, *A. & P. Felton & I. G.-de la Cerda 1854*, 30–9–1984, (DUKE); Clinton Co., Singlebranch Creek, *L. Stair*, 11–7–1944 (MICH). Vermont: Wallingford, *G. Kennedy*, 3–8–1907 (MICH). Virginia: Madison Co., Fisher's Gap and Rose Rvr., *I. Schnooberger 4740 & F. Wynne*, 15–6–1944 (MICH). West Virginia: Greenbrier Co., *H. Burtt*, Jun 1971 (MICH). Wisconsin: Willburn, *J. Röll 1635*, 16–12–1888 (as *A. attenuatus* var. *brevifolius*, G). Richland Co., Richland Center, *M. Nee 12059*, 13–6–1974 (MICH).

Cuba. Pinar del Río: Baños San Vicente, *Britton 7446*, Aug–Sep 1910 (as *A. wrightii*, NY). **Dominican Republic.** Santiago: orillas del Guanajuma, San Cristóbal, *J. Jiménez M-7*, 16–4–1946 (NY). La Vega: Salto de Aguas Blancas, SW of Constanza, *W. R. Buck 7900*, 27–4–1982 (NY).

Austria. Küstenland: Görz, *K. Loitlesberger*, May 1911 (c. fr., NY). **Byelorussia.** *L. I. Savicz* (NY). **Denmark.** Ganloese: "near Copenhagen," *W. C. Steere & Holmen*, 21–7–1954 (c. fr., NY). **France.** Haute Garonne: Prat de Joueou, *Dismier 286*, 3–7–1928 (MA). Haute Savoie: Douvaine, "Boisé de Ballaison," *E. Bonnot 714*, 31–12–1962 (BCB). **Germany.** Oberbayern: Bayerbrunn, *Lewis*, 9–11–1845 (NY). **Hungary.** "Praeillycum, Sopianicum: Transdanubia Mts., Mecsek, Valle Nagymélyvöelgy," *I. Györffy*, 25–7–1923 (BCB). **Italy.** "Silva Montello" (NY); "Venetia, Monte Baldo" (ex herb. Thümen NY). Novocomo: Flaglearo, supra Varese, *F. A. Artaria*, 11–4–1897 (NY). **Norway.** Akershus: "Emmestad in Vestby," *P. Størmer*, 10–4–1950 (BCB). **Poland.** "Western Carpathians": Cieszyn, Dziegielow, *Jedrzejko & Zarnowiec*, 7–10–1981 (BCB). Kraków-Czestochowa Upland, "Sokole Góry," 15 km SE of Czestochowa, *H. Bednarek -Ochyra & R. Ochyra*, 21–6–1986 (MICH). **Russia.** Karelia: inter Petrosavodsu et Kosalma, *H. Baukoh*, 20–7–1973 (NY). **Spain.** Barcelona: Santa Fe de Montseny, *Casas*, 26–3–1969 (BCB). Castellón: Fuente La Reina, *Herrero-Borgoñón 341*, 16–5–1982 (MA). Girona: vall de Vidrà, *I. G.-de la Cerda 2345 & F. Lloret*, 28–3–87 (BCB). Huesca: Cañón de Añisclo, Fanlo, *I. G.-de la Cerda 2216 et al.*, 15–8–1986 (MA). Lleida: val d'Aràn, Portilló de Bossost, *C. Casas*, 3–6–1977 (BCB). Navarra: Selva de Irati, *A. Ederra*, 25–3–1982 (NAU). Rioja: Sierra de la Demanda, hayedo de Tobía, *M. Brugués*, 28–6–1977 (BCB) (see Granzow-de la Cerda, 1988a). **Sweden.** Uppsala: *Mosén*, Oct 1866 (NY). Øland: St, Dalby, *No. 974* 3/6–8–1969 (MICH). **Switzerland.** Zug, *Bamberger* (NY). Genéve: "bois de Frontenoy, prés de Genéve," 15–1–1853 (NY). **Ukraine.** "Ditio Chmelnitski, Kamenets-Podalsk," *M. Kotov*, 23–7–1948 (NY). "Ditio Kioviensis, pr. Bila Tzerkva," *D. Zerov*, 24–5–1926 (NY).

Anomodon attenuatus is a polymorphic species. Plants from the Pyrenees, for instance, are very reduced in size. The distinctive attenuate branches, for which the species is named, are sometimes arcuate and seldom ascending; however, sometimes in some specimens the branch apices become slightly capitate and incurved. Robust plants of *A. attenuatus* might be mistaken for *A. viticulosus,* because both have acute leaf apices. They can be told apart by their branch morphology: ascending and robust in *A. viticulosus*, and prostrate and complanate in *A. attenuatus*. Also, the leaf shape is different in both species: lanceolate and without constriction in *A. attenuatus*, but lingulate and abruptly narrowed from a broadly ovate base in *A. viticulosus*. The costa in *A. attenuatus* also lacks the thick, seriate papillae on the dorsal surface. A consistent character in fertile plants of *A. attenuatus* is the absence of gametangia beyond the most recent branching points (i.e., they are never formed on the youngest branches).

The name *A. wrightii* has been used for specimens from the Caribbean islands (the type specimen collected from Cuba), but they agree with *A. attenuatus*.

15. Anomodon giraldii Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 3: 91. 1896.—TYPE: CHINA. "China interior, provincia Shen-si septentr.," 1894, *Giraldi*, det. C. Müller, nr. 1032 (holotype: FI!). Fig. 29.

Plants moderately robust, forming loose mats, yellowish green to brown; plants irregularly pinnate; central strand not differentiated; primary branches to 6 cm long, 0.9–1.3 mm thick when dry, profusely branched; secondary branches attenuate, inserted close to each other on primary branches in a whorl-like fashion, or successively in a stairlike fashion; branches arcuate, recurved, and often thickened at the end; flagelliform branches with reduced leaves present. Branch leaves erect to erect-spreading when moist, 1.5–2.5 mm long, 1.0–1.4 mm wide, strongly decurrent, secund, somewhat falcate near the apex and concave to keeled because of a prominent costa, ovate-lanceolate, acute, widest at 1/3 from the base, margins almost straight from that point to the apex, without constriction, usually revolute, plicate in the basal half. Costa strong, prominent on the abaxial side, pellucid, flexuose in the distal half, percurrent or ending very near the apex (<0.1 mm), thickened at the end; cells of the costa rather short (almost as short as laminal cells, rarely >11µm long, 17 µm closer to the base), on the dorsal surface smooth or, mostly toward the apex, with numerous, randomly arranged minute papillae. Laminal cells pellucid, not isodiametric but irregularly rectangular, basal cells not papillose, walls strongly sinuose, often porous, gradually merging with the upper cells; upper cells with somewhat sinuose walls, papillae multiple, simple and short on both surfaces. Perichaetia few, with abundant paraphyses, absent beyond the most recent branching points. Perichaetial leaves long and narrow, smooth, costa absent or very reduced. Seta 7–20 mm. Capsules cylindrical, erect or slightly curved; urn 2–3 mm, with some stomata, annulus absent; operculum rostrate, ca. 1/3–2/3 the length of the urn; exostome ca. 0.3 mm high, smooth at the base, teeth finely papillose above; endostome consisting of a basal membrane several cells high, 0.1 mm, segments rudimentary. Spores (12–) 16–23 (–25) µm in diameter, smooth to very finely papillose. Chromosome number unknown.

Distribution (Fig. 26). Japan (the four large islands), China (Hunan, western Hubei, Chensi, Manchuria, Yellow Sea coast), Korea (Cheju Island included), Far Southeast Russia; restricted to the Yellow Sea and Sea of Japan region as well as to the Chensi Mountains (*locus classicus*). According to Iwatsuki (1963), *A. giraldii* usually grows on rock substrates, acidic and basic, including stone walls, also on tree trunks and rotten logs. This species can be dominant in epiphytic communities in montane deciduous forests, where it forms thick and extensive mats. Sporophytes have seldom been collected (Iwatsuki recorded only six fertile collections).

REPRESENTATIVE SPECIMENS. **China.** Hubei: "Shennongjia, Forest District," *Sino-Amer. Exp. 665*, 3–9–1980 (NY, FH, HIRO, MICH). Hunan: Hsikwangschan mines, pr. Hsinhwa, *Handel-Mazzetti*, May 1918 (NY, FH, JE). Jiangxi: Mt. Lu-Shan, *C. K. Tung*, Jun 1955 (JE). Liaoning: distr. Benxi, Yangchi, *Guo Qian 8435 & Zhang Guang Chu*, 6–7–1963 (IFSBH); distr. Feng Cheng, Feng Huang shan, *Guo Qian 6889*, 29–5–1963. **Japan.** Etehu, Ohsho-mura, *H. Sasaoka*, Apr 1917 (JE), Ohyama, Kaminii kawa, *Sasaoka* (c. fr., herb. Chamberlain FH); Mt. Bandai, *E. Uematsu*, May 1908 (JE);

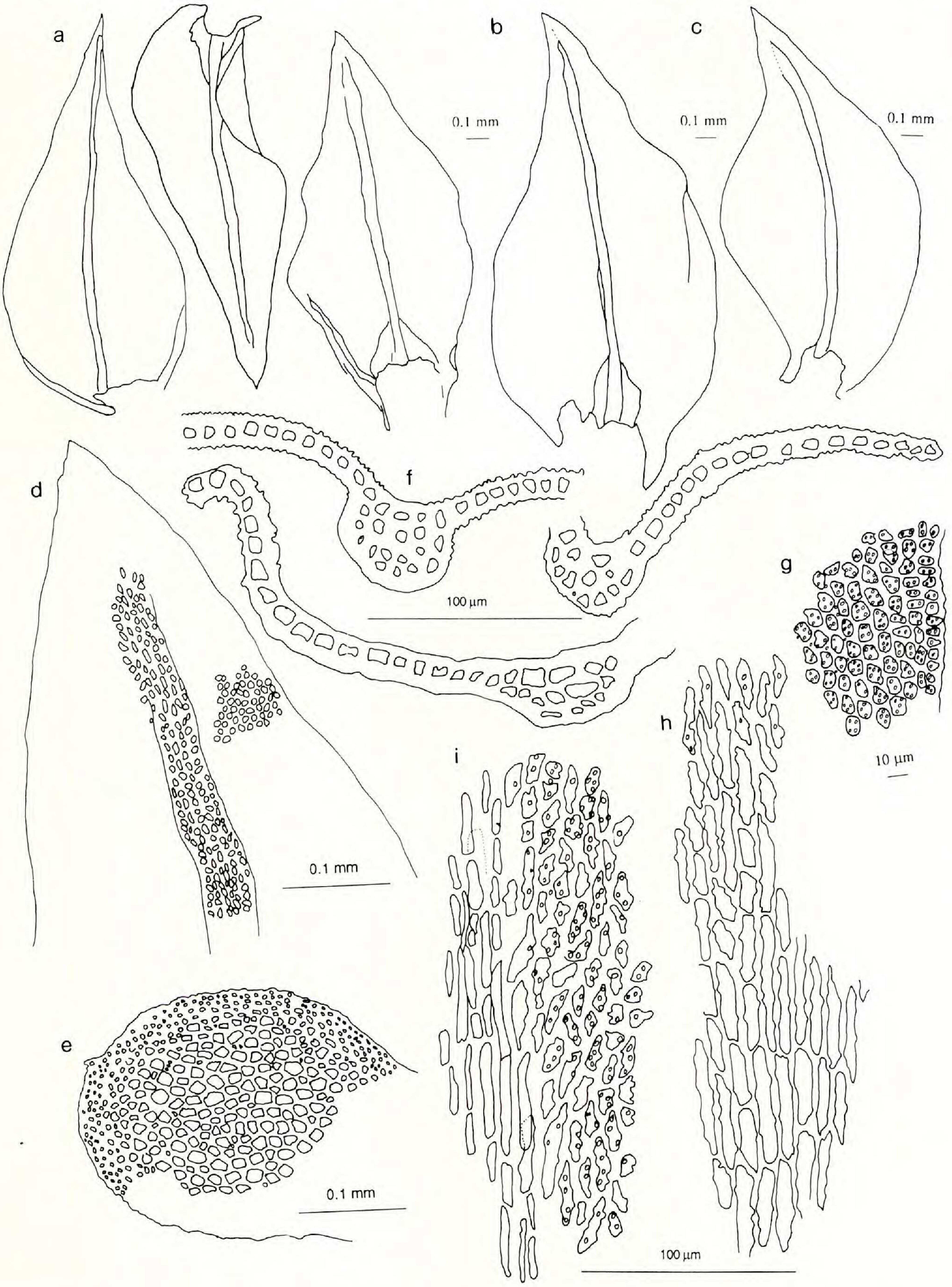


FIG. 29. *Anomodon giraldii* Müll. Hal. a–c, branch leaves; d, leaf apex; e, cross section of stem, without differenciated central strand; f, cross sections of leaves; h, group of hyaline basal cells of the leaf; i, cells of costa at mid-leaf; g, cells of leaf margin near the apex. Based on: a, *Iwatsuki 9574*, Japan, "Kyushu, Miyazaki-ken, Higashi-usuki-gun" 26–5–1981 (NY); b, i, *H. Sasaoka*, Japan, Echizau, Goka, Jul 1921 (FH); c, d, *Lazarenko*, Russia, "Asia Bor. Orien. in regio austro-ussuriensis, fl. Ssputinka" Oct. 1934 (FH); e, *Iishiba*, Japan, Sendai, 7–9–1907 (DUKE); f–h, *S. Murai*, Japan, "Akita pref., Mt. Taiheizan, Ninbetsu Nat. Forest," 1–4–1968 (NY).

Miyadzu, *Faurie 1518*, 1901 (NY); Sendai, *E. Iishiba*, 7–9–1907 (DUKE). Hokkaido: Ishikari distr., Sapporo, Tenguyama, *T. Koponen 21488*, 8–07–1971 (herb. Chamberlain FH), Kamuikotan, *A. Noguchi*, 21–8–1951 (JE, MICH, NY). Honshu : Akita pref., Akita, Mt. Taiheizan, *S. Murai*, 1–4–1968 (NY); Aomori pref., Shirikari, *K. Kikizaki 5*, 18–5–1977 (NICH), "Yunosawa valley," *K. Kakizaki*, 27–7–1976 (DUKE); Ettyu, Mt. Kurobe, *H. Sasaoka*, 7–6–1930 (herb. Chamberlain FH); Gifu pref., Ono-gun, Nomugi-toge pass, *H. Katsuyama 13166*, 25–5–1968 (NICH); Hiroshima pref., Iwaidani valley, *R. Watanabe 23496*, 24–8–1976 (NICH); Inaba, Mt. Kyushu-zan, *H. Ochi*, 17–4–1955 (herb. Bartram FH); Iwate pref., Mt. Aoba, *S. Nakamishi*, 21–7–1960 (JE), Shinoehei-gun, Iwaizumi-cho, *R. Watanabe 17035*, 23–8–1972 (NICH), Rikutuyu, Mt. Iwate, *G. Joba 224*, 29–6–1928 (NY); Kyoto pref., Oecho, Naigu, *M. Mizutani*, 7–10–1967 (NY, c. fr., JE, MICH); Mt. Komona, *K. Mureta*, 9–6–1918 (herb. Sasaoka DUKE); Mie pref., Inabe-gun, Mt. Fujiwara-dake, *H. Katsuyama 4593*, 20–4–1969 (NICH); Miyagi pref., Isl. Kinkazan, *M. Mizutani*, 6–9–1959 (NICH); Nagano pref., *N. Takaki*, 27–6–1949 (NY), Kisofukushima., *Schofield 51961*, 7–10–1972 (DUKE); Niigata pref., *Y. Ikegami* Mar 1948 (JE, MICH); Saitama pref., Chichibu-gun, Ashi-ga-kubo, *R. Watanabe 23576*, 11–10–1976 (NICH); Shimane pref., Iishi-gun, Akaana Shrine, *M. Higuchi 13939*, 17–5–1987 (c. fr., HIRO); Tottori pref., Mt. Daisen, *T. Koponen 21841*, 20–07–1971 (herb. Chamberlain FH); Yamagushi pref., Iwakuni, Shiroyama, *Schofield, Ando & Seki 54512*, 16–4–1973; "Echizand, Goka," *H. Sasaoka*, Jul 1921 (herb. Brotherus FH); "Hida, Mt. Kotori," *H. Sasaoka*, Aug 1918 (herb. Brotherus FH); Taisyayu, *A. Noguchi*, Jun 1932 (herb. Bartram FH). Kyushu: Bungo, Mt. Kudy, *A. Noguchi*, 4–11–1934 (herb. Bartram FH); Fukuoka pref., Asakura-gun, *Y. Kuwahara 2361*, 23–11–1951 (NY); Kumamoto pref., Mt. Fukabayama, *N. Takaki 2888*, 23–4–1932 (NY), Kuma, Mt. Taiheizan, *K. Mayebara*, 4–4–1952 (DUKE), Kohnox, *K. Maebara, 3810* 20–9–1955 (NICH), Mt. Aso, *H. Shojima 1575*, 25–4–1970 (NICH); Miyazaki pref., Higashi-usuki-gun, *Z. Iwatsuki 9574*, 26–5–1981 (NY); Nagasaki, *Wichura 1461* (as *A. acutifolius*, NY); Oita pref., Mt. Kurodeke, pr. Kakushimizu, *Z. Iwatsuki 290a*, 30–10–61 (c. fr., NICH). Shikoku: Ehime pref., Kami-ukena-gun, Tengu-Kogen platteau, *Z. Iwatsuki 5245 & H. Kiguchi*, 23/24–8–1978; Tokushima pref., Miyoshi-gun, Mt. Tsurugi, *R. Watanabe 19134*, 22–8–1973 (NICH). **Korea.** Kong Ouen to, *Faurie 4052*, Jul 1907 (FI), Mt. Chiak, *W. Hong 5875 5876, 5879, 5878* (c. fr.), 16/17–7–1961 (NICH), Mt. Haura, *W. Hong 2246*, 7–8–1960 (NICH), Mt. Kwan-ak, *W. Hong 1518*, 27–3–60 (NICH), Mt. Odai, *W. Hong 2567, 2570, 2608*, 24–10–1960 (NICH), Mt. Sokri, *W. Hong 2795, 2817*, 21–12–1960 (NICH), Isl. Dagelet, *W. Hong 6121, 6123*, 26/29–7–1961 (NICH). Cheju: "Ile Guelpaert," *Faurie 303*, 1906 (NY). **Russia.** Ussuriisk, "Regio austro ussurensis: flumen Ssputinka," *A. Lazarenko* ex herb. Verdoorn 254, Oct 1934 (FH, JE, MICH), ibid., *L. Bardunov*, 9–9–1962 (NICH); distr. Partizanskyi, pr. Lozovyi, *L. Bardunov & V. Tcherdantzeva*, 13–9–1974 (NICH).

Flagelliform branches are common in *A. giraldii*. Some branches, however, bear reduced leaves or are leafless at the middle, while the leaves near the apex are of a regular size. *Anomodon giraldii* resembles *A. attenuatus* in its branching pattern and attenuate branch apices, but it is readily distinguishable from any other species in the genus by its ovate-lanceolate leaves without constriction, its lax areolation of rectangular leaf cells with sinuose walls, especially near the leaf base, and the multiple, unbranched, rather small papillae. *Anomodon giraldii* and *A. attenuatus* are, moreover, allopatric in distribution.

This species is named after Father Giuseppe Giraldi, an active collector in China and Japan, who provided Carl Müller with the type specimen.

16. Anomodon longifolius (Brid.) Hartm., Handb. Skand. Fl. ed. 3, 300. 1838. *Pterigynandrum longifolium* Schleich. ex Brid., Mant. Musc. 128. 1819. *Leskea longifolia* (Brid.) Spruce, Musc. Pyren. n. 87. 1847. *Hypnum longifolium* (Brid.) Müll. Hal., Syn. 2: 474. 1851.—Type: unknown. Fig. 30.

Anomodon armatus Broth., Hedwigia, 38: 243. 1899.—Type: Japan. Hokkaido, 29–4–1894, Oiwake, *Miyabe & Tokubuchi 392* (syntype: FH!).

Plants somewhat slender, growing in rather thick mats, yellowish green, with branches 20–30 (–60) mm long, 0.5–1 mm thick when dry. Stems with filamentous and foliose pseudoparaphyllia, rhizoids abundant above (especially in Japanese

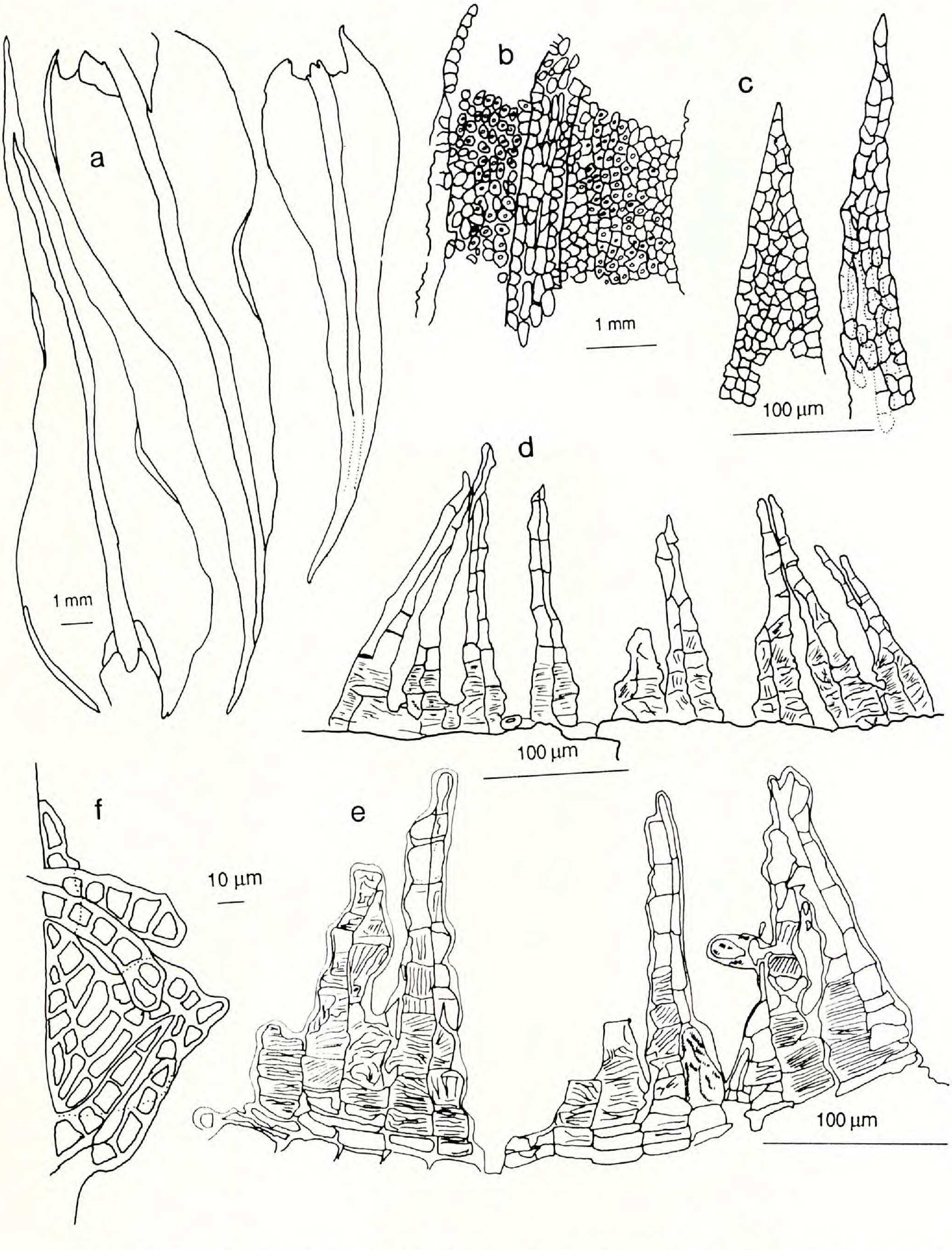


FIG. 30. *Anomodon longifolius* (Brid.) Hartm. a, branch leaves; b, surface of a leaf; c, branch leaf apices; d, e, portions of exostome; f, branch "bud" showing pseudoparaphyllia. Based on: a–f, from herb. J. Ångtröm, Sweden, Sala, "sub. Pterog." (NY).

material); branches profuse, fasciculate or irregularly pinnate; secondary branches usually attenuate, often flagelliform, apices frequently club-shaped and/or recurved, central strand of stem well differentiated. Branch leaves 2.1 mm long (to 2.8 mm or more), 0.3–0.5 (–0.6) mm wide at the base, quite densely arranged, secund, clearly falcate, almost recurved when dry and somewhat plicate at the base, in robust forms; in smaller, more delicate plants the leaves 1.2–1.6 mm, julaceous and more imbricate when dry; branch leaves decurrent, narrowing more or less abruptly below the middle (0.2–0.35 mm at the widest above the shoulders) and tapering into a subulate apex, often 2–3 cells wide at the end; margins revolute near the shoulder, entire to serrulate and often with shorter and wider cells near the apex; costa yellowish, somewhat decurrent, protruding and making the leaf carinate, often scabrous on the back in the upper half, percurrent, with dorsal cells noticeably shorter and incrassate, as long as those of the lamina (7–11 µm); basal cells near the costa generally not hyaline, smooth, longer than those of the rest of the lamina, the basal group extending less than 1/4 the length of the leaf base; medial laminal cells ca. 15 µm long, with a single, central, rather high papilla on both surfaces, which never exceeds the cell's diameter. The youngest perichaetia and perigonia on the most distal portions of the branches usually with minute or flagelliform branches extending beyond the inflorescences; perigonial leaves smooth, areolation lax; cells of perichaetial leaves isodiametric and smooth near the apex. Seta yellow, 4–8 mm; urn 1.2–1.7 (–2.0) mm, elongate, cylindrical, exothecial cells hexagonal-isodiametric, stomata absent; annulus absent; operculum conic to short-rostrate, ca. 0.5 mm, somewhat asymmetric, obtuse; exostome irregular, 0.25–0.30 mm, striolate at the base; endostome rudimentary (0.08–0.13 mm), generally reduced to a short pellucid basal membrane, 1–2 cells high, sometimes bearing a few scattered very slender segments of the same height. Spores 12–17 µm in diameter. Chromosome number unknown.

Distribution (Figs. 14, 15, 18). Throughout most of Europe, except in Ireland, Portugal, and the Mediterranean islands, to the Caucasus; also in Japan (Hokkaido and Honshu) and Russia's Far East; absent from the New World. *Anomodon longifolius* grows generally on rocks but sometimes on tree bark.

REPRESENTATIVE SPECIMENS. **Azerbaijan.** Bakuriani, *Lazarenko & Abramov*, 5–9–1956 (NY). **Georgia.** "Tzenis Tzchali, Svania Dadianosum, Hippi, inter Muri et Lentec," *Sommier & Levier*, 29–7–1890 (NY). **Japan.** Asorezan, *Faurie 2095*, 1902 (c. fr., NY); Borezan, *Faurie*, 11–10–1902 (herb. Bartram FH). Hokkaido: Kamuikotan, *A. Noguchi*, Aug 1951 (MICH); Rikuku, Mt. Hakkoda, *E. Iishiba*, Jul 1907 (MICH), Mutsu, *S. Okamura*, 31–7–1913 (NICH); Ishicari, Yamabe, *Z. Iwatsuki*, 7–8–1971 (exicc. Noguchi 1202, MICH, NY); Sapporo, Isiskaki, *N. Iwasaki 4704*, 16–10–1914 (NY); Si-Kari, Kamikawa-gun, *Takenauti 1432*, 10–03–1919 (NY). Honshu: Kominato, *Faurie 49*, 9–12–1889 (FI); Mt. Shirouma, *N. Takaki*, 1–08–1949 (NY); Fukushima pref., Otakine, Oniana, *T. Higuchi*, 3–10–1958 (exicc. Noguchi, NY); Nagano pref., Shimotakai-gun, Sakai-mura, *S. Okamura*, 28–10–1913 (NICH), *S. Uto* (?), 23–10–1913 (FI), Kijimadaira, *K. Saito*, 3–8–1972 (MICH); Shimano, Mt. Tagakushi, 1–8-1908 (FH); Tottori pref., Mt. Mitoku, *H. Ochi*, 12–6–1960 (NY).

Austria. Markenstein, *E. Berroyer*, 2–5–1869 (MICH). Wien, *E. Berroyer*, 16–3–1869 (NY). Salzburg: bei Hallstadt, *J. Fraehlich*, 16–3–1869 (NY). Steyermark: Altenessen, *Th. Suse*, 12–8–1910 (ex herb. Uggla NY). **Belgium.** Frahan, *Delogne 82*, Mar 1869 (NY); Namur, Feyr, May 1874 (NY). Comunne de Yvoir: Bauche, *De Sloover 30206*, 1–4–1979 (NY). **Byelorussia.** Minsk, *L. Savicz*, 23–5–1923 (NY). **Finland.** Pohjois-Pohjanmaa, Tervora, Peu, *T. Ulvinen*, 16–7–1977 (NY). "Ostrobotnia kajonensis": Paltamo, *M. Lindvquist*, 18–7–1931 (NY). Pohjois-Saavo: Kuopio, Sükalahti, *A.J. Huuskonen*, 3–9–19661 (NY). "Savonia borealis": Kaavi, Likosaari, *A. Teräsvuori*, 22–6–1917 (NY). Tohmajärvi, Havukkavaara, S of Vuorenpää, *R. Fagerstén & M. Haapasaari 4095* (MICH), *4097*, 2–10–1984 (as *A. viticulosus*, FH). Siilinjärvi: Iso-Pettäinen, Kourulahti Bay, *R. Fagerstén 776*, 30–7–1974 (MICH). **France.** Haute Savoie: Reignier, *Puejet*, Nov (NY). Isère: Baigns-la-Romaine, *De Sloover 35014*, 25–7–1981 (MICH, NY). Jura: Jouhe, Foulotière, *P. Cuynet 114–116*, 5–5–1960 (BCB). Savoie: Aux-les-Bains, *J. Müller* (NY). **Germany**. Pr. Baierbrunn, *P. G. Lorentz*, 1860 (c. fr., ex herb. Uggla NY). Allgäu: Hinterstein, Bärgündele Bach, *De Sloover 16494*, 8–9–1973 (NY). Bayern: Berchtesgaden, *Th. Suse*, 6–9–1895 (ex herb. Uggla NY); Nagelfluhblöchen, Bayernbrunn, München, *A. Holler*, Oct 1861 (NY). Mont Rhön: *Geheeb*, 1879 (NY). Thuringia: Müstberg, *H. Möller*, Apr 1859 (ex herb. Uggla NY). Wartburg, *V. Rüsse* (NY). **Hungary.** Comit. Pest, Madencia, pr. Ocsa, *Boros*, 14–10–1928 (NY). Comit. Bereg: pr. tarpa, *A. Boros*, 15–3–1961 (BCB). Comit. Heves: Mte.

Agasvár, pr. Nagybátony, *Boros*, 6–5–1928 (NY). **Poland.** Montes Gorce, Kamienica, *Lisowski*, 18–4–1959 (Bryot. Polon. 1114 NY). Kielce: Montes Góry, Swietokrzyskie, *Lisowski 64989*, 1–6–1964 (NY). Krosno: "W Bieszczady mnts., Kurników Beskid," *R. Ochyra*, 7–7–1977 (BCB, MICH). Bialystok: Puscza Augustowska, *Lisowsky 68685*, 30–10–1958 (NY, MICH). Schlesien [Silesia]: Breslau, *J. Milde* (NY). Suwalki: Smolniki, Lake Jaczno, *R. Ochyra*, 17–5–1979 (MICH), Lake Haneza, *R. Ochyra*, 18–5–1979 (MICH). **Russia.** Göbersdorf, Friedland [Pravdinsk], *J. Milde*, 30–7–1868 (NY). Karelia: "Karelia ladogensis, Suistamo, Saarisuonvaara," *A. J. Hueskonen*, 24–8–1935 (NY); "Karelia onegensis, Uksjärvi, Kossalmi," *M. J. Kotilainen*, 9–6–1942 (NY). Moscow : Ruza distr., Ozhigovo, *M. Ignatov*, 11–6–1988 (MICH), Kunzowo, "pr. Mosquam," *Meyden*, 22–4–1899 (NY). Kursk: Karotscha Dean, *Lawdanski*, 19–9–1902 (NY). "Sibiria," Jenisei, Nikulina, *H. Arnell*, 18–7–1876 (NICH). **Spain.** Barcelona: Sta. Maria de Besora, *C. Casas*, Dec 1964 (BCB). Navarra: Sierra de Urbasa, *A. Ederra*, 13–3–1982 (BCB, NAU). **Sweden.** Ångermanland: Säbrå, Grövhall, *H. W. Arnell*, 1–6–1870 (NY). Närke: Svenshyttan, *C. Hartman*, 31–10–1874 (NY). Öland: Högbyn, Vyksjö, *Hj. Möller*, 25–7–1917 (DUKE), Mariehamn, *H. Möller*, 26–7–1928 (NY). Vestetad Lund, *K. Holmen*, 8–6–1969 (NY). Östergötland: Marmosbruket, *P. Olsson*, 23–6–1875 (NY). Sala: "sub Pterog" (c. fr., ex herb. Sullivant NY). Skåne: Öveds su, Fruelid, *G. Ålberg*, 15–6–1919 (ex herb. Uggla NY). Småland: Greunabruket, Vretaholm, *A. Arvén*, 18–5–1914 (NY); Talberg, *N. Schentz* (herb. Thümen NY). Torshunda, *H. Möller*, Apr 1859 (herb. Uggla NY). Uppsala: Gottsundabergen, *J. Zettersstedt 95*, 7–5–1878 (MICH), Uppsala, 1844 (herb. Thümen NY). Västmanland: Sala Gruva, 31–5–1879 (DUKE). **Switzerland.** Pr. Zürich, *P. Culmann*, Apr 1885 (NY). Valais: Lonèche-les-Bains, *H. Fossell*, Sep 1887 (NY). Zug: Prope Zug, *Bamberger 6522*, 1855 (NY). **Ukraine.** pr. Kiev, Holossijevo, *N. Wagner*, 16–3–1919 (NY). **United Kingdom.** Gloucestershire, Forest of Dean, *H. N. Dixon*, 20–7–1903 (NY). Wales: Somerset, *C. H. Bisnstead*, 4–12–1886 (NY).

Anomodon longifolius can hardly be mistaken for any other species in the genus. Distinctive characters are the presence of pseudoparaphyllia (shared only with *A. rugelii*), the incrassate, isodiametric, irregular or shortly rectangular cells on the back of the costa, and the irregularly striolate exostome (in some specimens alternating with finely punctate areas, sometimes smooth above, sometimes divided into two filaments, which are generally verruculose-papillose). Specimens of *Leskeella nervosa* (Brid.) Loeske are rather often found misidentified as *A. longifolius*, probably due to their remarkably similar appearance. The leaf cells of *Leskeella*, however, lack papillae, its costa does not extend toward the apex as far as in *A. longifolius*, and its marginal cells are shorter and more elliptical; the leaves of *L. nervosa* are more crowded, julaceous (not secund), and more acuminate than subulate.

In some specimens of *A. longifolius*, branches of two kinds may appear: robust branches with leaves to 2.1 (–2.8) mm long, crowded, secund, clearly falcate, almost recurved when dry and somewhat plicate at the base, as well as more delicate branches, with leaves 1.2–1.6 mm long, julaceous, and more imbricate when dry.

Anomodon armatus Broth., described from Japan, coincides in every feature with western material and is here included in *A. longifolius*.

Herpetineuron (Müll. Hal.) Cardot, Beih. Bot. Centralbl. 19(2): 127. 1905. *Anomodon* sect. *Herpetineuron* Müll. Hal., Flora 73: 496. 1890.—TYPE: *Herpetineuron toccoae* (Sull. & Lesq.) Cardot.

Bryonorrisia Stark & Buck, Brittonia 38: 52. 1986.—TYPE: *Bryonorrisia secunda* (Dixon & Badhw.) Stark & Buck [=*Herpetineuron acutifolius* (Mitt.) Granzow].

Plants rather robust, forming open to thick mats. Stems prostrate, sparsely branching; branches rather arcuate, circinate or, often, attenuate toward the apex, with a well-differentiated central strand of smaller cells, without paraphyllia or pseudoparaphyllia. Branch leaves incurved, secund when dry, erect, not complanate when moist, ovate-lanceolate, tapering from the base, without an obvious constriction; margins flat, serrate in the distal 1/3–1/4; apex sharply acuminate; costa single, strong, pellucid, smooth on the back, not obscured by laminal cells, ending sharply at or near the apex, not bifid at the tip; laminal cells practically not differentiated throughout the lamina, rectangular to rhombic, slightly longer than wide, smooth, sometimes prorulate, walls somewhat thickened. Seta 8–16 mm. Capsule erect, cylindrical to elliptic or almost symmetrical, urn 1.5–2.8 mm, annulus well differentiated; peristome relatively well developed, exostome striolate at the base, endostome papillose with a basal membrane 1–4 cells high, segments 0.2–0.4 mm high, papillose. Calyptra smooth. Chromosome number unknown.

Herpetineuron is undoubtedly the genus most closely related to *Anomodon*, at the core of the Anomodontaceae; they both lack paraphyllia and have a relatively undeveloped peristome. The endostome in the two species of *Herpetineuron* here recognized is, nonetheless, somewhat more developed than those of most species of *Anomodon*. The lack of leaf cell papillae in *Herpetineuron* must be regarded as a derived trait. Stark and Buck (1986) created the genus *Bryonorrisia* when they removed *B. secunda* from *Forrstroemia* and assigned it to the Anomodontaceae, and stated that it strongly resembles *Herpetineuron*. Enroth (1991) also acknowledged the close relationship of *Herpetineuron* and *Bryonorrisia*, but argued that both genera belong in the Leskeaceae. I do not see a sufficient reason, based either on gametophytic or sporophytic morphology, to segregate *Bryonorrisia* from *Herpetineuron*. Whether the Anomodontaceae are closest to the Leskeaceae or to the Thuidiaceae, or should be subordinated to either of them, has been an ongoing and unresolved argument (see Introduction). I feel more at ease with the placement suggested by Anderson et al. (1990), or at least with that of Buck and Crum (1990), in which the family Anomodontaceae, *Herpetineuron* included, is considered to be close to the Leucodontaceae.

The generic name refers to the snakelike costa, characteristic of *H. toccoae*, the type species.

KEY TO THE SPECIES OF HERPETINEURON

1. Costa strongly flexuose-sinuose in the distal 2/3 of the lamina; lamina smooth throughout. 1. *H. toccoae*.

1. Costa straight throughout; back of the distal 1/2 of the lamina with prorulate cells. 2. *H. acutifolium*.

1. Herpetineuron toccoae (Sull. & Lesq.) Cardot, Beih. Bot. Centralbl. 19(2): 128. 1905. *Anomodon toccoae* Sull. & Lesq., Musci Bor. Amer. 52. 1856.—TYPE: U.S.A. Georgia: Toccoa Falls, *C. L. Lesquereux*, Musci Bor. Amer. exsicc. 1, *240* (isotypes: G! MICH! NY!).

Anomodon devolutus Mitt., J. Linn. Soc. Bot., suppl. 1: 127. 1859.– SYNTYPES: CHINA. Hong Kong, *Bowring*; INDIA. Mehra, "11.000 ft.," *Thomson*, 23-7-1848; Simla, "7000 ft.," Thomson 10/49 (syntypes, NY-herb. Mitten!).

Anomodon wichurae Broth., Hedwigia 39: 244. 1899. *Herpetineuron wichurae* (Both.) Cardot, Beih. Bot. Centralbl. 19(2): 128. 1905.—TYPE: JAPAN. Kiushiu, Nagasaki, *Wichura 1461a* (isotype: NY).

Herpetineuron formosicum Broth., Ann. Bryol. 1: 22. 1928.—TYPE: TAIWAN. Prov. Taityn, Hori, *Suzuki* (n.v.).

Herpetineuron attenuatum S. Okamura, J. Coll. Sci. Imp. Univ. Tokyo 38(4): 54. 1916.—TYPE: Japan. Hondo, Prov. Sagomi, Kamakura, 1–3–1914, *Hisauchi* (n.v.).

Plants rather robust, in open, dull, dark greenish to yellowish brown mats. Stems prostrate, sparsely branching; branches (1–) 2–4 cm long, (0.2–) 0.9–1.3 mm thick when dry, rather arcuate, terete when dry, branching pattern often consisting of several orders of successive branching in a stepwise fashion, circinate or, often, attenuate toward the apex, with a well-differentiated central strand of smaller cells, without paraphyllia or pseudoparaphyllia. Branch leaves incurved, secund, involute in a tubular fashion when dry, erect, not complanate when moist, ovate-lanceolate, tapering from the base, without an obvious constriction, 1.8–2.8 mm long, 0.5–1.2 mm wide; margins flat, irregularly and strongly serrate in the distal 1/3–1/4, serrations consisting of 1 to several cells; apex sharply acuminate; costa single, strong, pellucid, almost always sinuose in the distal 1/3, smooth on the back, not obscured by laminal cells, ending sharply at or near the apex, not bifid at the tip; laminal cells ± homogeneous throughout the lamina, rectangular to rhombic, slightly longer than wide, smooth, walls somewhat thickened. Perichaetia found on youngest branches; perichaetial leaves 1.5–2.2 mm, flexuose-subulate, often somewhat crispate, laminal cells smooth throughout. Seta 14–16 mm, light reddish brown. Capsule erect, almost symmetrical, yellow to reddish brown; urn (1.7–) 2.0–2.8 mm, stomata few, cells at mouth and annulus well differentiated; operculum conic; peristome fairly well developed, exostome ca. 0.5 mm high, papillose and faintly striolate at the base and above, endostome papillose with a basal membrane to 3–4 cells high (0.05–0.15 mm), segments 0.2–0.3 mm high, papillose throughout. Spores 16–22 µm in diameter, densely papillose. Chromosome number: n = 11 (n = 9+H+h, in mitosis, Japan: Inoue 1965).

Distribution (Fig. 24). *Herpetineuron toccoae* is widely distributed in temperate as well as tropical regions. In the New World *H. toccoae* is present and somewhat common in the mountains of North and South Carolina, Georgia, and Tennessee, in the Ozarkian Highlands, in scattered localities in southern Illinois, western Florida, Louisiana, eastern Texas, Mexico, Guatemala, Honduras, Nicaragua, the Dominican Republic, and SE Brazil. In the Old World it occurs in the Himalayas and southern India, Sri Lanka, Manchuria and southeastern China, Korea, Japan, Vietnam, the Philippines, Celebes, Sumatra, Java, and New Caledonia (Norris & Sharp 1961). According to Brotherus (1925), *H. toccoae* is present in South Africa and West Africa, and Kis (1985) cites five references from Tanzania. The species is absent in Europe and Central Asia. *Herpetineuron toccoae* grows on trees, sometimes at their base, or occasionally on rocks. It forms rather thick mats in temperate, deciduous, mostly montane forests. It never fruits in North America.

REPRESENTATIVE SPECIMENS. **China.** Fukien: Buong Kang, Yenping, *H. Chung*, 14–6–1925 (DUKE); Kushan, pr. Foochow, *H. Chung B-240a*, 17–8–1925 (c. fr., DUKE MICH). Kwangtung: Jen hwa distr., Man Chi Shan, *Tsang W.T. 26178*, Apr 1936 (c. fr., MICH). Hong Kong: *J. C. Bowring* (as *Anomodon devolutus*, syntype, herb. Mitten NY); Kowloon, Panlong wan, *Y. W. Taam 2007*, 9–6–1941 (DUKE); New Territory, Taimoshan, Chunloong, *Y. W. Taam, 1948*, 16–3–1941 (c. fr., MICH). **India.** Kumaon, *J. Duthie 6367*, 22–8–1886 (MICH). Madras distr: Pulney Hills, Kodaikanal (coll. ignot. Nr. 88), Jan 1957 (DUKE). NW Himalayas: Mt. Nag Tiba, *Rhada Sal*, 7–12–1900 (as *A. devolutus*, DUKE). **Japan.** Sendai, *E. Iishiba 3046*, 20–10–1907 (DUKE). Miyazaki pref., Nao, S of Nichinan, *W. Schofield 53094-3*, 9–1–1973 (DUKE); Oita pref., Takeda-machi, *A. Noguchi*, 1–12–1947 (DUKE). **Japan.** Goto. *Faurie 1596*, 1901 (as *H. wichurae*, NY). Prov. Higo: Konase, Kuma-gun, *K. Mayebara 96*, 14–10–1928 (as *H. wichurae*, NY). Honshu: Mie pref., Yoro fall, *N. Takaki 5291* (as *H. wichurae*, NY).

Brazil. Santa Catarina, Bom Retiro, BR 282, *Schäfer-Verwimp 10483 & Verwimp*, 21–12–1988 (MICH). Rio de Janeiro, *Glaziou 9155, 9216, 9222* (as *Anomodon brasiliensis*, NY). **Guatemala.** Huehuetenango: W of Aguacatán, *P. Standley 81215*, 27–12–1940 (MICH). **Honduras.** Comayagua: Río Selguapa, 4 km SE of Siguatepeque, *B. Allen 11800*, 11–5–1992, *13403*, 2–3–1993 (MO). Olancho: nr. Catacamas, *R. Olson 83-8*, 22–9–1983 (MO). **Nicaragua.** Estelí: Salto de Estanzuela, 6 km S of Estelí, *D. Stevens 11754*, 1–10–1979 (MO). **Mexico.** Chiapas: "above Las Casas," *A. Sharp 3365*, 20–4–1945 (MICH). Chihuahua: Chupie, *H. LeSueur A4b*, 20–8–1937 (MICH). Durango: El Salto, *A. Sharp 1895a*, 31–12–1994 (MICH). Guerrero: Omiltemi, 30 km W of Chilpancingo, *A. Sharp 1135b*, 27–10–1944 (MICH). Jalisco: La Ferrería, above Manatlán, *H. Crum 984a, 790*, Jul 1949 (MICH). México: Temascaltepec, Ixtapan, *G. Hinton 2937a*, 14–12–1932 (MICH). Morelos: Cerro Tepozteco, *C. Delgadillo*, 28–9–1991 (MEXU). Nuevo León: Sierra Madre Or., Monterrey, SW of El Cercado, *F. Hermann 26082*, (MICH). Oaxaca: Tamazulapan Mixé, *A. Sharp 2990 et al.*, 23–12–1972 (MICH). Puebla: "below Necaxa," Río Tenango, *A. Sharp 3124*, 26–3–1945 (MICH); Río Necaxa, pr. Huanchinango, *A. Sharp 3142*, 27–3–1945 (MICH). San Luis Potosí: Xilitlá *A. Sharp 5911*, 22–4–1946 (MICH). Sinaloa: W of Las Palmitas, *D. Norris 20358 et al.*, 25–5–1971 (MICH). Sonora: pr. El Tigre, Rancho del Roble, *S. White 4229*, Sep 1941 (MICH). Tamaulipas: Sierra de Guatemala, S of Rancho del Cielo, *H. Crum 1664, 1690*, Aug 1950 (MICH). **U.S.A.** Alabama: Winston Co., Bankhead Nat. For., *W. Buck 21869* (MICH, NY). Arizona: Sycamore Canyon, nr. Ruby, *I. Haring 3297 & H. Skell*, 11–3–1945 (NY). Arkansas: Cleburne Co., nr. Greer's Ferry Reserv., *P. Redfearn 18729 & F. Bowers*, 12–3–1966 (MICH, NY). Garland Co., Hot Springs Nat. Pk., *L. Anderson 11347*, 5–10–1953 (DUKE, MICH). Georgia: Stephens Co., *J. Small*, 8–8–1893 (G, DUKE, MICH), *L. Anderson 22078*, 28–7–1975 (DUKE, MICH). Illinois: Union Co., Panter's Den, *P. Redfearn 23407*, 24–1–1968 (MICH). Louisiana: Tangipahoa Par., Tangipahoa Rvr., E of Ponchatoula, *W. Reese & G. Landry 17011*, 30–10–1986 (as *Haplohymenium triste*, MICH). West Feliciana Par., pr. St. Francisville, *W. Reese 10843*, 3–4–1969 (MICH). Mississippi: Oktibbeha Co., S of Starkville, *S. McDaniel 5542*, 4–1–1965 (MICH, NY). North Carolina: McDowell Co., Linville Caverns, *L. Anderson 11024*, 14–7–1952 (DUKE, MICH). Jackson Co., Whitewater Falls, *I. G.-de la Cerda 1297*, 13–6–1984 (BCB). Tennessee: Sevier Co., trail from Greenbrier to Brushy Mt., *A. Sharp & P. Voth 349*, 29–3–1936 (MICH).

Dominican Republic. Azúa: Cañada Miguel Martín, *M. Mejía & T. Zanoni 8267*, 18–9–1980 (MO).

Herpetineuron toccoae is distinguished by the sinuose costa near the leaf apex. It is unmistakable in its habit when dry: a large, usually epiphytic moss forming thick mats, with the leaves falcate-secund and strongly incurved. The distinctive costa inspired Cardot to name the genus *Herpetineuron* ("snake costa"); however, the second species lacks a sinuose costa.

2. Herpetineuron acutifolium (Mitt.) Granzow, Bryol. 92: 385. 1989. *Anomodon acutifolius* Mitt., J. Linn. Soc. Bot., suppl. 1: 126. 1859. *Bryonorrisia acutifolia* (Mitt.) Enroth, J. Bryol. 16: 407. 1991.—TYPE: INDIA. Uttar Pradesh, Kumaon 6000, Sarkito Shayuk valley, *800* (lectotype, designated by Enroth, 1991: NY-herb. Mitten!). Fig. 31.

Forrstroemia secunda Dixon & Badhw., Rec. Bot. Surv. India 12: 176. 1938. *Bryonorrisia secunda* (Dixon & Badhw.) Stark & Buck, Brittonia 38: 52. 1986.—TYPE: INDIA. "Dalhousie," *Badhwar 339* (holotype: BM).

Plants moderately robust, branches fasciculate or irregularly pinnate, arcuate, often attenuate and flagelliform, 0.5–0.7 mm in diameter when dry. Stem and primary branch leaves secund and wider, those of secondary branch leaves narrower and julaceous when dry, triangular-lanceolate, 1.3–1.8 mm long, sometimes somewhat secund and asymmetric, without mid-leaf constriction, decurrent, always acute, margin flat and entire but becoming serrulate just at the apex; costa decurrent, weak, straight, ending sharply 0.2–0.35 mm, or sometimes more, from the leaf apex, cells of costa elongate, longer than laminal cells; lamina cells shortly rectangular or rhomboidal, heterogeneous in size and orientation, smooth but some prorulate on the abaxial surface. Male gametangial buds borne proximally

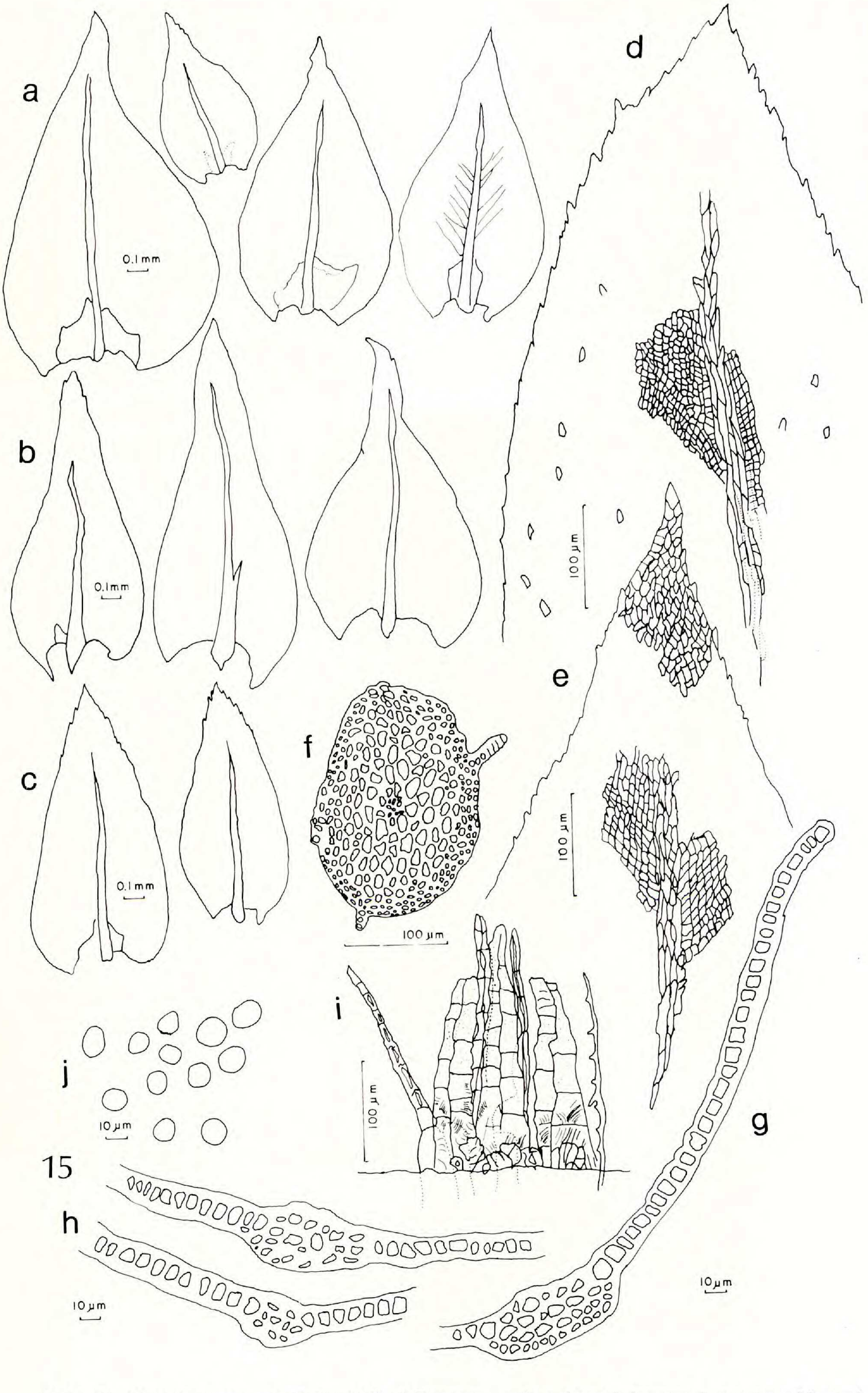


FIG. 31. *Herpetineuron acutifolius* (Mitt.) Granzow. a, b, c, branch leaves; d, e, apex of branch leaves; f, cross section of stem with differenciated cells in the center; g, h, branch leavers in cross section; i, portion of peristome with well-developed endostome; j, spores. Based on: a, f, h, *Falconer & Royle*, India, NW Himalaya (NY); b, d, g, j, *Koeltz* 7529, India, Punjab, Kangra, Bathad, (FH); c, e, i, *Strachey & Winterbottom 70/13*, India, Kumaon, above Jallet, (NY).

from the last branching points, but female gametangial buds borne proximally as well as distally. Perichaetial leaves acute with the apex strongly serrate. Seta 8–9 mm. Capsules cylindrical or elliptic; urn 1.5–2.2 mm; exostome well developed, horizontally striolate at the base, teeth trabeculate, endostome well developed, basal membrane 1–3 cells high, segments long, filiform. Chromosome number unknown.

Distribution (Figs. 22, 28). Unlike *H. toccoae*, *H. acutifolium* has a rather narrow, although disjunct distribution. It occurs in the Himalayas, southern China, Taiwan, and Japan, and is also known from two localities in the state of Chihuahua, Mexico.

REPRESENTATIVE SPECIMENS. **China.** Yunnan: Diancang Mt. Range, *P. Redfearn & Y.G . Su 1520*, 18/20–7–1984. **India.** Himachal Pradesh: Simla, *Bell* 113 (NY), "7–8000 ft," *Thomson*, Oct 1849 (NY) Punjab: Kangra, Kulu, Bathad, *W. Koeltz 7529*, 24–11–1933 (FH). Uttar Pradesh: Kumaon, Naintal, *A. Norkett 11851*, 4–10–1966 (as *Herpetineuropsis secunda*, NY); Kumaon, above Jallet, 7500', *Strachey & Winterbottom 70/13* (syntype of *H. acutifolium*: NY-herb. Mitten!), Kathi 7000', *Strachey & Winterbottom 70/43* (syntype of *H. acutifolium*: NY-herb. Mitten!); Rampur-Bushahr, Dorkali, *W. Koeltz 3185d*, 29–11–1931 (NY); "NW Himalaya," *Falconer & Royle* (NY). **Japan.** Honshu: Saitama pref., Chichibu, Mt. Akazawa-dake, *Nagano 5021*, 9–9–1953, *Nagano 10991*, 28–9–1957, *Nagano 9816*, 7–8–1957 (NICH). **Nepal.** East Nepal: "between Dor and Chauke," *Z. Iwatsuki 421, 431*, 7–6–1972 (NICH); "between Topke Gola and Shewaden," *Z. Iwatsuki 1899*, 28–6–1972 (NY, HIRO). Katmandu: Mt. Phulchoki, "summit area," *Z. Iwatsuki 2670*, 15–7–1972 (NICH).

Mexico. Chihuahua: "51 mi of Creel," La Junta to Creel, *F. Bowers et al.*, 31–12–73 (with *H. toccoae*), 4–1–1974 (MEXU); "30 min. N de San Juanito" *C. Delgadillo*, 4–1–1974 (MEXU).

Herpetineuron acutifolium reminds of *A. attenuatus* and *A. girandii* in its habit, because they too have attenuate and often flagelliform branches. However, *H. acutifolium* differs entirely in its leaf and cell morphologies from any species of *Anomodon*, including the absence of a leaf constriction and the smooth leaf cells. The habit and branching pattern, as well as the triangular-lanceolate leaf outline and serrulate apex, are very similar to that of *H. toccoae*. The costa, unlike that of *H. toccoae*, is not sinuose but slender and decurrent at the base, but the areolation is almost identical in both species. Cells are rhomboidal, sometimes with scattered prominent cells on the laminal surface. The peristome and especially the endostome are rather well developed in both species, more than in any species of *Anomodon*; the segments are narrow but strong, as long as the exostome teeth, perforate, and rising from a very low basal membrane (Granzow-de la Cerda 1989). Enroth (1991) transferred *H. acutifolium* to *Bryonorrisia*, based on its more developed peristome.

EXLUDED NAMES

Anomodon californicus Lesq., Mem. California Acad. 1: 30. 1968. ≡ *Triquetrella californica* (Lesq.) Grout.

Anomodon brasiliense Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn, ser. 3, 4: 56. 1872. ≡ *Dimerodontium brasiliense* (Hampe) Broth., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26, Afd. 3: 50. 1900. ≡ *Myrinia brasiliense* (Hampe) Schimp., Gen. Sp. Musc. 2: 292. 1878.

Anomodon lagoensis Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn, ser. 3, 2: 238. 1870. ≡ *Leskea lagoensis* (Hampe) Gier, J. Bryol. 10:

211. 1978. = *Pseudoleskea subcatenulata* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 234. 1872. = *Rauia subcatenulata* (Besch.) Broth., Nat. Pflanzenfam. 1(3): 1005. 1907. = *Rauiella subcatenulata* (Besch.) Wijk. & Marg., Taxon 11: 222. 1962. ≡ *Rauiella lagoensis* (Hampe) Buck, Bryol. 94: 82. 1991.

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Anomodon nervosus (Brid.) Hüb., Musc. Germ. 561. 1833. ≡ *Leskeella nervosa* (Brid.) Loeske, Moosfl. Harz. 255. 1903.

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Anomodon scaberrimus Broth., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 21, Afd. 3: 65. 1895. ≡ *Macrocoma scaberrima* (Broth.) Vitt, Bryol. 82: 16. 1979.

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Haplohymenium densum Schimp., Mém. Soc. Sci. Nat. Cherbourg 16: 233. 1872. = *Leskea mexicana* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 233. 1872. = *Lindbergia mexicana* (Besch.) Cardot, Rev. Bryol. 37: 51. 1910.

TAXA NOT AVAILABLE FOR STUDY

Anomodon grandiretis Broth., Akad. Wiss. Wien Sitzungsber., Math.-Naturwiss. Kl., Abt. 1. 133: 578. 1924.

Haplohymenium tenuissimum (Besch.) Broth. (*Pseudoleskea tenuissima* Besch.). According to the description and distribution, this name is most likely a synonym of *Haplohymenium pseudotriste* (see also Noguchi, 1957).

Haplohymenium magnirete Sakurai, Bot. Mag. (Tokyo) 64: 196, 1c, d. 1951.

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APPENDIX 1

CHARACTER CODING

The list of characters used in the cladistic analyses is given below, with an explanation for each of the states coded. The two species of *Herpetineuron* and *Pterigoneuron gracile* were used for character polarization. Undetermined states (coded as "?") represent one of the three following scenarios: the state is not known for a particular taxon; the character does not apply (i.e., the taxon lacks the structure which is referred to); or the taxon shows polymorphism for a given character (when not resolvable by including more than one state in the matrix, using the notation, for example, "1&2"). Whether the multiple-state characters were ordered or not is indicated for each. Character 11 was "partially ordered" using a predefined state matrix.

1. Branching pattern (unordered; Fig. 1). 0 = Primary stem with simple branches in a loose pinnate arrangement. 1 = Primary stem with secondary branches bearing tertiary branches in a pseudofasciculate fashion, tuftlike; the tertiary branches are erect and arise from the secondary branches very close to each other, appearing whorled (e.g., *A. longifolius* and *A. rostratus*). 2 = As in state 1, but also with the secondary branches bearing branches, usually arcuate, of several successive orders, in a stairstep fashion (e.g., *A. attenuatus* or *A. giraldii*).

2. Attenuate and/or flagelliform branches. 0 = Absent. 1 = Present.

3. Cross section of the stem. 0 = Central strand of conspicuously smaller cells well differentiated. 1 = The stem homogeneous in cross section, without a differentiated central strand of smaller cells.

4. Pseudoparaphyllia. 0 = Absent. 1 = Present.

5. Branch leaf arrangement when dry (ordered). 0 = Erect to julaceous. 1 = Secund. 2 = Conspicuously incurved.

6. Orientation of branch leaves when moist (ordered). 0 = Not flattened on either the ventral or the dorsal side of secondary branches. 1 = Flattened only on the dorsal surface of secondary branches, while secund and pointing to the substrate on the ventral surface. 2 = Flattened on both surfaces, especially towards the end of secondary branches.

7. Leaf constriction. 0 = No distinguishable constriction; leaves lanceolate to triangular-ovate (e.g., *A. giraldii*). 1 = Constriction present ("shoulders"), more or less abruptly dividing the leaf into a broad lanceolate proximal region and a narrow distal one.

8. Leaf length. 0 = Small: <0.7 mm long. 1 = Large: >1.4 mm long.

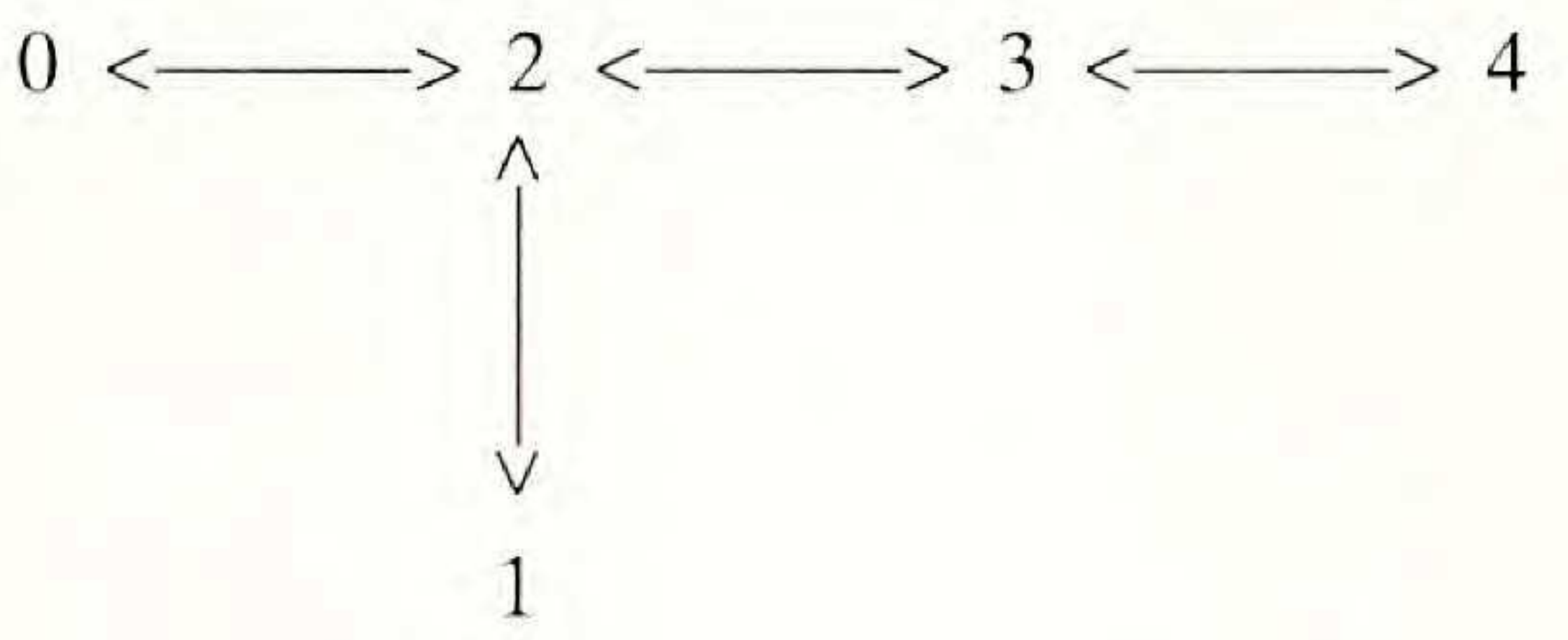
9. Shape of the distal region of the lamina of branch leaves, above the shoulders (Fig. 2). 0 = Tapering, i.e., with margins never parallel but progressively narrowing between shoulders and apex. 1 = Portions of the lamina above the shoulders as narrow as the apex (or even narrower, as in *A. minor*), i.e., with margins parallel at least in some portions. ? = For species without a distinct shoulder. Note: in *A. viticulosus* the character presents a polymorphism within mats.

10. Leaf margin. 0 = Plane throughout. 1 = Revolute in part.

11. Shape of branch leaf apex (partially ordered; Fig. 3). 0 = Leaves tapering into a multiseriate subulate apex, in *A. longifolius*. 1 = Leaves abruptly ending in a sharp and long uniseriate acumen (*A. rostratus*). 2 = Acute (*A. giraldii*). 3 = Acute to obtuse, in the same plant. 4 = Rounded to obtuse, but never acute. Note: The leaf apex is often short-apiculate in *A. rugelii*, although the outline of those leaves is essentially obtuse or rounded. Such an apiculum is not at all uniseriate and not even acute; therefore, it is not at all similar to that of *A. rostratus*.

12. Leaf margin near the apex. 0 = Entire, although sometimes slightly crenulate due to the presence of papillae. 1 = With teeth.

Transformation Series (Character Tree)



Step Matrix

	0	1	2	3	4
0	-				
1	2	-			
2	1	1	-		
3	2	2	1	-	
4	3	3	2	1	-

13. Length of the costa (ordered; Fig. 4). 0 = Not reaching beyond the lower 1/3 of the leaf lamina. 1 = Reaching to 2/3–3/4 of the length of the leaf. 2 = Reaching ca. 9/10 of the leaf length to subpercurrent.

14. Costa bifid near the apex (Fig. 5). 0 = Never bifid. 1 = Costa becomes bifid just at the apex (although one of the branches often much shorter), at least in some leaves on a mat. ? = Character polymorphic among stems within mats (*A. attenuatus* and *P. gracile*).

15. End of the costa covered by laminal cells. 0 = Well defined throughout, ending sharply, not obscured by laminal cells. 1 = Costa not ending sharply, somewhat fading as laminal cells cover it, but only at the end. 2 = Upper part of the costa totally obscured by overlaying laminal cells, starting as far down as the level of the leaf constriction, or just above it.

16. Papillae on cells of dorsal surface of the costa (unordered; Fig. 6). 0 = Cells smooth or with very discrete vesicle-like bumps. 1 = Papillae minute, numerous and randomly arranged on each cell (e.g., *A. giraldii*). 2 = 4–7-seriate, tall papillae per cell, not branched. ? = Cannot be scored for *Anomodon tristis* because of its small size and obscured costa.

17. Papillae on basalmost margin cells, at the insertion of the leaf (ordered). 0 = Lacking papillae, or with papillae numerous, but always similar to other laminal cells. 1 = Intermediate: one or two somewhat mamillose cells may appear at the margin. 2 = Cells with very prominent papillae, larger than those on laminal cells, usually single and sometimes branched, resembling spines.

18. Shape of leaf cells, at least those toward the middle of the lamina. 0 = Elongate: rhombic or rectangular. 1 = Isodiametric: hexagonal, quadrate or round.

19. Leaf cell papillae (unordered). 0 = Absent. 1 = One central large papilla, pointed, arcuate, (sometimes with 1–3 small branches at the base), entirely covering cell lumen. 2 = One central short papilla, rounded, entirely covering cell lumen. 3 = Multiple, unbranched, very short papillae. 4 = Multiple, scarcely to strongly branched papillae.

20. Position of gametangial buds relative to most recent (distal) branching points (ordered; Fig. 7). 0 = The most recent gametangial buds appear distally, relative to the last branching points (i.e., perichaetia or perigonia develop on the youngest branches). 1 = Only flagelliform branches are produced beyond gametangial buds (e.g., *A. longifolius* and *Herpetineuron acutifolium*). 2 = Gametangial buds never found distally relative to latest branching points but only on stem or older branches.

21. Cells of perichaetial leaves. 0 = Smooth throughout. 1 = Papillose, at least near the leaf apex.

22. Length of seta (ordered). 0 = >4 mm. 1 = 1.5–3 mm. 2 = <1 mm (capsule immersed). ? = Sporophytes unknown for *A. dentatus* and *A. flagelliformis*.

23. Length of urn. 0 = <1.1 mm. 1 = >1.3 mm. ? = Sporophytes are unknown for *A. dentatus* and *A. flagelliformis*; length is highly variable in *A. giraldii*.

24. Stomata. 0 = Present. 1 = Absent. ? = No information is available for *A. dentatus*, *A. solovjovii*, and *A. flagelliformis*.

25. Annulus. 0 = Well developed. 1 = Poorly differentiated. ? = Sporophytes unknown for *A. dentatus* and *A. flagelliformis*.

26. Exostome structure. 0 = Teeth more or less reduced, irregular or incomplete, <0.20 mm long. 1 = Teeth splitting more or less symmetrically, >0.25 mm long. ? = Polymorphic in *A. pseudotristis*; unknown for *A. dentatus* and *A. flagelliformis*.

27. Striolate ornamentation at base of exostome. 0 = Absent. 1 = Present. ? = No information is available for *A. dentatus*, *A. flagelliformis*, and *A. giraldii*.

28. Papillose ornamentation at the base of exostome. 0 = Absent. 1 = Present. ? = No information is available for *A. dentatus*, *A. giraldii*, and *A. flagelliformis*, and there is a polymorphism in *A. longifolius*.

29. Ornamentation at upper part of exostome teeth (unordered). 0 = Verrucose, with thick bumps unevenly arranged. 1 = Papillose, with papillae evenly distributed. 2 = Smooth or finely rugose. ? = Sporophytes are unknown for *A. dentatus* and *A. flagelliformis*.

30. Segments of endostome (ordered). 0 = Absent or almost absent (0–1 cells high). 1 = Present but short (3 or more cells high). 2 = Well developed, almost as high as exostome teeth. ? = Sporophytes are unknown for *A. dentatus* and *A. flagelliformis*.

31. Calyptra. 0 = Glabrous. 1 = With a few long and scattered hairs. ? = Sporophytes and calyptra are unknown for *A. dentatus* and *A. flagelliformis*.

LIST OF SYNONYMS

Anoectangium ferrugineum Besch., Ann. Sci. Nat., sér. 7, Bot. 17: 329. 1893. = A. rugelii.

Anomodon aculeatus Broth. & Paris, Rev. Bryol. 31: 56. 1904. = A. longinervis.

A. acutifolius Mitt., J. Linn. Soc. Bot., suppl. 1: 126. 1859. = H. acutifolium.

A. apiculatus B.S.G., Bryol. Eur., fasc. 44–45. 1850 (nomen nudum) = A. rugelii.

A. armatus Broth., Hedwigia, 38: 243. 1899. = A. longifolius.

A. asperifolius Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 3: 117. 1896. = A. abbreviatus.

A. attenuatus var. *brevifolius* Ren. & Cardot, Hedwigia 32: 302. 1893 (nomen nudum) = A. attenuatus
A. attenuatus.

A. brevinervis Broth., Öfver. Finsk. Vet. Soc. Förh. 33: 107. 1891. = A. preudotristis.

A. decurrens Cardot, Bull. Soc. Bot. Genève, sér. 2, 3: 281. 1911. = A. viticulosus.

A. devolutus Mitt., J. Linn. Soc. Bot., suppl. 1: 127. 1859. = H. toccoae.

A. exilis Mitt., J. Linn. Soc. Bot. 13: 309. 1873. = A. preudotristis.

A. ferrugineus (Besch.) Nog., J. Jap. Bot. 20: 260. 1944. = A. rugelii.

A. filiformis Thw. & Mitt., J. Linn. Soc. Bot. 13: 308. 1873. = A. preudotristis.

A. fragilis Wilson, London J. Bot. 7: 275. 1848. = A. tristis.

A. fragillimus Herzog, Beih. Bot. Certralbl. 26: 82. 1909. = A. tristis.

A. glossophyllus Müll. Hal. in Paris, Ind. Bryol. suppl. 14. 1900 (nomen nudum) = A. minor.

A. huttonii Mitt., J. Linn. Soc. Bot. 13: 309. 1873. = A. preudotristis.

A. integerrimus Mitt., J. Linn. Soc. Bot., suppl. 1: 126. 1859. = A. minor.

A. leptodontoides Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 4: 275. 1897. = A. minor.

A. microphyllus Broth. & Paris, Rev. Bryol. 31: 56. 1904. = A. tristis.

A. minor (P.-Beauv.) Lindb., Bot. Not. 1865: 126. 1865 (nom. illeg.) = A. minor.

A. minor subsp. *integerrimus* (Mitt.) Z. Iwats., J. Hattori Bot. Lab. 26: 41. 1963. = A. minor.

A. minor var. *inaequalifolius* Bartr., Bryologist 50: 207. 1947. = A. minor.

A. mithouardii Paris & Broth., Rev. Bryol. 29: 97. 1902. = A. preudotristis.

A. obtusifolius Bruch & Schimp., London J. Bot. 2: 668. 1843 (nom. superfl.) = A. minor.

A. obtusifolius Mitt. (nomen nudum) [non *A. obtusifolius* Bruch & Schimp.] = A. viticulosus.

A. obtusifolius var. *w* Mitt., (nomen nudum) = A. thraustus.

A. planatus Mitt., J. Linn. Soc. Bot., suppl. 1: 126. 1859. = A. minor.

A. platyphyllus Kindb., Ottawa Naturalist 7: 19. 1893. = A. minor.

APPENDIX 2. Data matrix used for the cladistic analysis: 19 taxa, 31 characters. (ord.) = unordered character; (p. ord.) = partially ordered, step matrix given in Appendix 1.

	Characters																														
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
A. viticulosus	0	0	1	0	1	0	1	1	0&1	0	3	0	2	1	0	2	1	1	4	0	1	0	1	1	0	0	1	0	2	1	0
A. rugelii	0	0	1	1	2	1	1	1	1	0	4	0	2	1	0	0	2	1	4	0	1	0	1	0	1	0	0	1	2	0	0
A. minor	0	0	0&1	0	0	2	1	1	1	0	4	0	2	1	0&1	2	1&2	1	4	0	1	0	1	1	0	0	0	1	1	0	0
A. thraustus	0	0	0	0	0	0	1	1	1	0	4	0	1	0	2	2	0	1	4	0	1	0	1	1	0	1	0	1	1	1	0
A. dentatus	0	0	1	0	0	0	1	1	1	0	3	1	2	0	2	0	0	1	4	0	1	?	?	?	?	?	?	?	?	?	?
A. abbreviatus	0	0	1	0	1	0	1	1	1	0	3	0	2	0	0	0	0	1	1	0	1	1	1	1	0	1	0	0	0	0	0
A. solovjovii	0	0	1	0	1	0	1	1	1	0	4	0	2	0	1	0	0	1	1	0	0	2	0	?	0	1	0	0	1	0	0
A. rostratus	1	0	0	0	0	0	1	0	0	1	1	0	1	0&1	1	2	0	0	4	0	0	0	0	0	0	1	1	0	1	2	0
A. attenuatus	2	1	1	0	1	2	1	1	0	1	3	1	2	1	1	0	1	1	4	2	1	0	1	0	1	1	1	0	1	2	0
A. giraldii	2	1	1	0	1	0	0	1	?	1	2	0	2	0	1	1	0	0	3	2	0	0	?	0	1	1	?	?	1	0	0
A. longifolius	1	1	0	1	1	0	1	1	0	1	0	0	2	0	1	0	0	0	2	1	0	0	1	1	1	0	1	?	0	1	0
Ha. triste	0	0	1	0	0	0	1	0	0	0	2	0	0	0	2	0	0	1	4	0	1	1	0	1	0	1	0	0	0	0	1
Ha. sieboldii	0	0	1	0	0	0	1	0	0	0	2	0	0	0	2	0	0	1	4	2	1	0	0	1	0	1	0	0	0	0	1
Ha. pseudotriste	1	0	1	0	0	2	1	0	0	0&1	3	0	0	0	2	0	0	1	4	0	1	1	0	1	0	?	0	0	0	0	1
Ha. flagelliforme	0	1	1	1	0	0	0	0	0	?	2	1	1	0	2	0	0	1	3	0	1	?	?	?	?	?	?	?	?	?	?
Ha. longinerve	0	0	1	0	0	1	1	0	0	0	3	0	1	0	2	0	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1
He. acutifolium	1	1	0	0	0	0	0	1	?	0	2	1	2	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	2	2	0
He. toccoae	2	1	0	0	1	0	0	1	?	0	2	1	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0
P. gracile	1	1	0	0	0	0	0	1	?	0	2	1	0	?	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0

1. branching pattern
2. flagelliform branches
3. cross section of stem
4. pseudoparaphyllia
5. leaf arrangement when dry (ord.)
6. orientation of leaves when moist (ord.)
7. leaf constriction
8. leaf length
9. shape of leaf distal portion
10. margin section
11. leaf apex (p. ord.)
12. margin outline near apex
13. costa relative length (ord.)
14. costa bifid at apex
15. costa fading
16. papillae back of costa
17. basalmost lf margin cells (ord.)
18. shape of leaf cells
19. leaf cells papillae
20. relative position of gametangial buds
21. perichaetial leaf cells papillose
22. length of seta
23. length of urn
24. stomata
25. annulus cells differentiated
26. exostome structure
27. base of exostome striolate
28. base of exostome papillose
29. ornamentation of upper teeth
30. segments
31. calyptra

A. plicaefolius Dixon (not validly published) = A. minor.
A. ramulosus Mitt., Trans. Linn. Soc. London, ser. 2, 3: 187. 1891. = A. minor.
A. rubiginosulus Müll. Hal., Flora 73: 496. 1890 (nom. superfl.) = H. toccoae.
A. rugelii var. *ferrugineus* (Besch.) Z. Iwats., J. Hattori Bot. Lab. 26: 51. 1963. = A. rugelii.
A. sinensi-tristis Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 3: 118. 1896. = A. tristis.
A. sinensis Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 3: 118. 1896. = A. minor.
A. solovjovii var. *henaensis* Tan, Boufford &Ying, Acta Bot. Yunnanica 18: 69. 1996. = A. solovjovii.
A. stenoglossus Cardot & Thér., Bull. Acad. Int. Géogr. Bot. 18: II. 1908. = A. preudotristis.
A. subintegerrimus Broth. & Paris, Rev. Bryol. 27: 77. 1900. = A. viticulosus.
A. submicrophyllus Cardot, Beih. Bot. Centralbl. 19(2): 128. 1905. = A. preudotristis.
A. toccoae Sull. & Lesq., Musci Bor. Amer. 52. 1856. = H. toccoae.
A. tonkinensis Besch., Bull. Soc. Bot. France, sér. 3, 41: 84. 1894. = A. viticulosus.
A. uematsui Broth., Öfver. Finsk. Vet. Soc. Förh. 62: 33. 1919–1920. = A. rugelii.
A. uyematsui Broth., Bull. Soc. Bot. Genève, sér. 2, 3: 281. 1911. = A. rugelii.
A. wichurae Broth., Hedwigia 38: 244. 1899. = H. toccoae.
A. wrightii Müll. Hal., Hedwigia 37: 262. 1898. = A. attenuatus.
Bryonorrisia acutifolia (Mitt.) Enroth, J. Bryol. 16: 407. 1991. = H. acutifolium.
B. secunda (Dixon & Badhw.) Stark & Buck, Brittonia 38: 52. 1986. = H. acutifolium.
Forrstroemia secunda Dixon & Badhw., Rec. Bot. Surv. India 12: 176. 1938. = H. acutifolium.
Haplohymenium biforme Broth., Bull. Soc. Bot. Genève, sér. 2., 3: 281. 1911. = A. longinervis.
H. brachycladum S. Okamura, Bot. Mag. Tokyo 25: 31. 1911. = A. sieboldii.
H. brevinerve (Broth.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907. = A. preudotristis.
H. crassum Sakurai, Bot. Mag. Tokyo 47: 337. 1933. = A. longinervis.
H. cristatum Nog., J. Jap. Bot. 20: 146. 1945. = A. flagelliformis.
H. fasciculare Nog., J. Jap. Bot. 13: 791. 1937. = A. preudotristis.
H. filiforme (Thw. & Mitt.) Broth., Nat. Pflanzenfam. 1(3): 1236. 1909. = A. preudotristis.
H. flagelliforme Savicz-L., Bot. Mater. Inst. Sporov. Rast. Glavn. Bot. Sada RSFSR. 1: 98. 101. 1922. = A. flagelliformis.
H. formosanum Nog., Trans. Nat. Hist. Soc. Taiwan 26: 43. 1936. = A. tristis.
H. fragiliforme Nog., J. Jap. Bot. 13: 410, f. 2. 1937. = A. tristis.
H. gonoi Broth., Öfver. Finsk. Vet. Soc. Förh. 62: 33. 1919–1920. = A. sieboldii.
H. huttonii (Mitt.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907. = A. preudotristis.
H. longiglossum P. C. Chen, Feddes Repert. Spec. Nov. Regni Veg. 58: 31. 1955. = A. tristis.
H. longinerve (Broth.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907. = A. longinervis.
H. microphyllum (Broth. & Paris) Broth., Nat. Pflanzenfam. 1(3) : 986. 1907. = A. tristis.
H. mithouardii (Paris & Broth.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907. = A. preudotristis.
H. mithouardii var. *viride* Thér., Ann. Crypt. Exot. 5: 179. 1932. = A. preudotristis.
H. nakajii S. Okamura, J. Coll. Sci. Imp. Univ. Tokyo 36(7): 26. 1915. = A. preudotristis.
H. obsoletinerve Broth., Öfver. Finsk. Vet. Soc. Förh. 62: 32. 1921. = A. preudotristis.
H. okamurae Cardot, Bull. Soc. Bot. Genève, sér. 2, 3: 281. 1911. = A. sieboldii.
H. pellucens Broth., Ann. Bryol. 1: 21. 1928. = A. sieboldii.
H. pellucens var. *obtusifolium* Broth., Ann. Bryol. 1: 21. 1928. = A. preudotristis.
H. piliferum Broth. & M.Yasuda, Öfver. Finsk. Vet. Soc. Förh. 62: 33. 1919–1920. = A. longinervis.
H. pinnatum Nog., J. Jap. Bot. 13: 410. 1937. = A. sieboldii.
H. pseudotriste (Müll. Hal.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907. = A. preudotristis.
H. sasaokae Broth., Classif. Moss. Japan: 149. 1932 (nomen nudum) = A. preudotristis.
H. scabrum Broth., Rev. Bryol. Lichénol. 2: 10. 1929. = A. tristis.
H. sieboldii (Dozy & Molk.) Dozy & Molk., Musci Frond. Arch. Indici 4: 127. 1846. = A. sieboldii.
H. spinosum Nog., J. Jap. Bot. 13: 789. 1937. = A. longinervis.
H. submicrophyllum (Cardot) Broth., Nat. Pflanzenfam. 1(3): 986. 1907. = A. preudotristis.

H. tenerrimum Broth., Rev. Bryol. Lichénol. 2: 10. 1929. = A. preudotristis.
H. triste (Ces.) Kindb., Rev. Bryol. 26: 25. 1899. = A. tristis.
Haptymenium viticulosum (Hedw.) Fürnr., Flora 10(2), Beilage 1: 81. 1827. = A. viticulosus.
Herpetineuron attenuatum S. Okamura, J. Coll. Sci. Imp. Univ. Tokyo 38(4): 54. 1916. = H. toccoae.
H. formosicum Broth., Ann. Bryol. 1: 22. 1928. = H. toccoae.
H. wichurae (Broth.) Cardot, Beih. Bot. Centralbl. 19(2): 128. 1905. = H. toccoae.
Hypnum attenuatum (Hedw.) Sm., Fl. Brit. 3: 1279. 1804. = A. attenuatus.
H. attenuatum var. *fulvum* (Brid.) Steud., Nomencl. Bot. 2: 252. 1824. = A. attenuatus.
H. fragile (Wilson) Müll. Hal., Syn. 2: 471. 1851. = A. tristis.
H. fulvum Brid., Musc. Rec. 2(2): 188. 1801. = A. attenuatus.
H. longifolium (Brid.) Müll. Hal., Syn. 2: 474. 1851. = A. longifolius.
H. pseudotriste Müll. Hal., Bot. Zeit. 13: 786. 1855. = A. pseudotristis.
H. rugelii Müll. Hal., Syn. 2: 472. 1851. A. = rugelii.
H. triste (Ces.) Müll. Hal., Syn. 2: 478. 1851. = A. tristis.
H. viticulosum (Hedw.) With., Syst. Arr. Brit. Pl. ed. 4, 3: 830. 1801. = A. viticulosus.
H. viticulosum var. *brachycarpum* Müll. Hal., Syn. 2: 473. 1851. = A. minor.
Leptohymenium longifolium Hampe, Syn. 1: 475. 1848 (nomen nudum) = A. longifolius.
L. sieboldii Dozy & Molk., Ann. Sci. Nat. Bot. sér. 3, 2: 310. 1844. = A. sieboldii.
Leskea apiculata Schimp. in Müll. Hal., Syn. 2: 473. 1851 (nomen nudum) = A. rugelii.
L. attenuata Hedw., Spec. Musc. 230. 1801. = A. attenuatus.
L. longifolia (Brid.) Spruce, Musc. Pyren. n. 87. 1847. = A. longifolius.
L. tristis Ces. in De Not., Syll. Musc. 67. 1838. = A. tristis.
Neckera flaccida Brid., Sp. Musc. 2: 137. 1812. = A. minor.
N. minor P.-Beauv., Prodr. 78. 1805. = A. minor.
N. sieboldii (Dozy & Molk.) Müll. Hal., Syn. 2: 81. 1850. = A. sieboldii.
N. viticulosa Hedw., Spec. Musc. 209. 1801. = A. viticulosus.
N. viticulosa var. *minor* Hedw., Spec. Musc. 210. 1801. = A. minor.
Pterigynandrum longifolium Schleich. ex Brid., Mant. Musc. 128. 1819. = A. longifolius.